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NON-RESIDENT LECTURESHIP IN CHEMISTRY
AT CORNELL UNIVERSITY

VOLUME 3

Muscular Movement in Man:
The Factors Governing Speed and Recovery from Fatigue

by

A. V. HILL

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BY

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ROYAL SOCIETY OF LONDON

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As I finished the pages of this book I heard of the passing of
a very gallant gentleman
ERNEST H. STARLING
Foulerton Research Professor of the Royal Society, sometime Jodrell Professor of Physiology at University College, London, well known and dearly loved in this country, as well as in his own. At the International Congress of Physiologists at Stockholm in 1926, Starling described Physiology as "the greatest game in the world." I had hoped to tell him of these experiments on runners, for he too knew something about running. This is forbidden, so I dedicate the account of them to his memory: and since he loved young men, and himself never grew old, he would be proud to have his name coupled with
THE ATHLETES AT CORNELL
whose friendly co-operation made them possible.

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PREFACE

The lectures on which this book is based were delivered during the Second Semester of 1926–1927 under the Non-Resident Lectureship in Chemistry which was endowed by Mr. George Fisher Baker of New York City.

I desire to extend to Professor Dennis and his colleagues my sincere and heartfelt thanks for the cordiality of their reception, and for the help which, on all occasions, they have been so ready to afford.

A. V. Hill.

Ithaca, New York, May 1927
Baker Laboratory of Chemistry.

INTRODUCTION

IN 1924, on the first evening I ever spent in America, I gave a lecture at the Franklin Institute in Philadelphia on "The Mechanism of the Muscle". Realizing the physical and engineering tradition of the Franklin Institute I told my audience what I could, in the brief space of an hour, about the inner working of that beautiful and mysterious machine. At the end, when questions were invited, I was asked, rather indignantly, by an elderly gentleman, what use I supposed all these investigations were which I had been describing. For a moment or so I stumblingly tried to explain what practical results might be expected to follow from a knowledge of how muscles work. There are practical consequences of course from all improvements of knowledge, as the history of science and invention tells. But to prove to an indignant questioner on the spur of the moment that the work I do was useful seemed a thankless task and I gave it up. I turned to him with a smile and finished—"to tell you the truth we don't do it because it is useful but because it's amusing". The answer was thought of and given in a moment: it came from deep down in my soul: and the results were as admirable from my point of view as unexpected. My audience was clearly on my side. Prolonged and hearty applause greeted my confession. My questioner retired shaking his head over my wickedness and the newspapers next day, with obvious approval, came out with headlines "Scientist Does It Because It's Amusing." And if that is not the best reason why a scientist should do his work I want to know what is. Would it be any good to ask a mother what practical use her baby is? That, as I say, was the first evening I ever spent in the United States and from that moment I felt at home. I realized that all talk about science purely for its practical and wealth-producing results is as idle in this country as in England. Practical results will follow right enough. No real knowledge is sterile. The most useless investigation

may prove to have the most startling practical importance: wireless telegraphy might not yet have come if Clerk Maxwell had been drawn away from his obviously "useless" equations to do something of more practical importance. Large branches of chemistry would have remained obscure had Willard Gibbs not spent his time at mathematical calculations which only about two men of his generation could understand. With this faith in the ultimate usefulness of all real knowledge a man may proceed to devote himself to a study of first causes without apology, and without hope of immediate return. He may even spend his time in observing what takes place in the muscles of frogs or in the bodies of athletes, confident in the hope that something of striking interest, possibly even of practical importance, may turn up.

I was invited by Professor Dennis to come to Cornell as a non-resident lecturer in Chemistry. Apparently, in Cornell, Chemistry is interpreted in a liberal and comprehensive sense: I was allowed to claim as chemistry the study of the processes that occur in the body of a man who is taking violent exercise. There is a plentiful supply of such men at Cornell, as indeed there is in England: in America, however, people are more inclined to treat the subject of athletics scientifically, and—astonishing to relate—are ready to recognize that what happens in the body of an athlete is "chemistry". So indeed it is—largely—though there are, I fear, many athletes and sportsmen in England who would be shocked by such any idea. Do not imagine that I suppose the whole of human life, all human endeavor, to be nothing but chemistry. There is, of course, much more in athletics than sheer chemistry, but it is founded on the basis of chemical reactions which can be examined in the laboratory. Battles at sea are won by heavy and accurate gun fire and well protected ships. In that sense engineering is the basis of naval tactics and one cannot understand the matter without recognizing the engineering aspects of it. No one, however, would be so foolish as to say that there is nothing else, no moral or intellectual qualities in those who man the guns, direct the fire, work the engines or decide the tactics. Just so it is in athletics. The machinery

of the body is all of a chemical or physical kind. It will all be expressed some day in physical and chemical terms. With this machine intelligent human beings have to work, aided by moral qualities of courage and resolution. Some will work their machinery better than others. Some will fail by lack of the necessary mental qualities, by lack of the necessary skill: some will neglect to keep their machinery in order. Others will fail for lack of resolution. The machine itself, however, has certain definite physical and chemical characters and if we neglect these we obviously cannot appreciate or understand the whole.

The complaint has been made to me—"Why investigate athletics, why not study the processes of industry or of disease?" The answer is twofold. (1) The processes of athletics are simple and measurable and carried out to a constant degree, namely to the utmost of a man's powers: those of industry are not; and (2) athletes themselves, being in a state of health and dynamic equilibrium, can be experimented on without danger and can repeat their performances exactly again and again. I might perhaps state a third reason and say, as I said in Philadelphia, that the study of athletes and athletics is "amusing": certainly to us and sometimes I hope to them. Which leads to a fourth reason, perhaps the most important of all: that being "amusing" it may help to bring new and enthusiastic recruits to the study of physiology, which needs every one of them, especially if they be chemists.

Professor Dennis has requested that I put these lectures into a book. It fortunately is possible for people to forget what is told them in a lecture: if you write it in a book it will be brought up against you in judgment later. Even lectures, however, are not safe. At a Christmas lecture at the Royal Institution I demonstrated a current intended to stimulate a frog's nerve by putting it through a loudspeaker: it was reported in the newspapers that "Professor Hill can cause nerves to make a noise like bagpipes" and "Punch" made the further comment "this is the only authentic information we have that there is any noise like bagpipes". I once told Dr. Vincent of the Rockefeller Foundation how, in 1924, on coming into New York Har-

bor I was fortunate enough to see the great German airship ZR-3 arriving overhead. He instantly remarked "two great gasbags from Europe blowing in at the same time." I have the impression that in this country people tend to like "gasbags from Europe"—at any rate they treat them as though they do. The astonishing thing is that they should desire their somewhat inert, if not rare, "gas" to be liquefied into a book: which is possible only if its temperature be very considerably lowered and its pressure raised. It is impracticable, anyhow, in a short period of four months,—especially in a place so hospitable and so beautiful as Ithaca—to give a series of lectures, to make a thousand new friends, to carry out researches on the material so plentifully supplied by Mr. John F. Moakley, and finally to write a book worthy of the name. So this is not a book, only a log of my visit to Ithaca. My friends must forgive its shortcomings: they helped to create them by their kindness.

CHAPTER I

Methods

THESE lectures are not to present the subject in its logical order, nor in the order in which the discoveries referred to were made. My intention is rather to make you interested in the physiology of muscle by introducing it to you through the medium of experiments on man. What is known about the science of muscular exercise in man—for it is becoming a science—is derived, in the first instance, from experiments previously made on lower animals, in many cases on the isolated muscles of such animals. Without this preliminary work we should still be in the dark as to the physical and chemical processes which accompany and cause muscular activity. But now that the preliminary work has been done—there is still a great deal to be learned in this way—it is possible to go on to that much more interesting animal, man, and to make observations which would be impossible without the intelligent co-operation of the experimental subject. After having in the first ten chapters discussed the case of man as the "Versuchstier" I will, in the remaining chapters, turn shortly to those experiments on the isolated muscles of animals from which many of these experiments on man have been derived. In this way I hope I may first be able to convince you that there is an important problem to hand, and then to interest you in the difficult physical and chemical questions which are raised by the power which muscle possesses of transforming chemical energy into mechanical work, at constant temperature, with so high an efficiency. Fundamentally this is a branch of thermodynamics, which needs chemists for its elucidation.

Not so long ago physiology, at least so far as it was presented to medical students, was concerned mainly with the properties of the frog. Books on "Human Physiology" referred largely to that animal. In recent years, owing to a great extent to the work and inspiration of

J. S. Haldane of Oxford, many new experiments on man have become possible which have thrown a flood of light on the workings of the body. Inasmuch as we all have bodies, we all ought to be to some extent physiologists, and recent work on the physiology of man has been largely concerned with certain things of which we are all well aware, circulation, respiration, muscular effort, consumption of food and energy, and so on. For this reason it is not so difficult to an audience of scientific people, mainly perhaps chemists, to dive straight into the subject without any logical introduction.

The human body is a machine—at any rate it possesses a number of machine-like properties. It obtains energy from food. The principle of the conservation of energy applies to it as it does to other machines. The following data may be useful:—

1 Calorie = energy required to warm 1 kilogram of water 1°C (at 15°C)
= 426.5 kilogram—meters
= 3086 foot-pounds.

The oxidation of one gram of fat in the body yields about 9 Calories of energy: of carbohydrate, about 4 Calories: of protein (to urea, carbon dioxide, water, etc.) 4 to 5 Calories. From these data the amount of energy in a man's diet can be calculated. Since a man doing sedentary work requires about 3000 Calories per diem, while one doing hard muscular work needs 6000 Calories or more, the amount of food that each requires can be calculated. Other factors determine how the different constituents should be apportioned.

In muscular work there is strong evidence that the immediate fuel which is oxidized is glycogen, $(C_6H_{12}O_6)_n$, a polymer of glucose. This, in its wet state, has a heat of combustion of 3.836 Calories per gram. Thirty grams of this substance (= CH_2O) requires 22.4 liters of oxygen for its oxidation. Thus 1 liter of oxygen, used in burning glycogen, has a definite energy value:—

1 liter oxygen = 5.14 Calories
= 15860 foot-pounds.

Fortunately all the other foodstuffs give approximately the same value, about 5 Calories per liter of oxygen. For example, cane sugar gives 5.07 Calories. Fat gives slightly less, but a measurement when that is possible of the "respiratory quotient" (volumes of carbon dioxide produced divided by volumes of oxygen used) tells us what particular mixture of foods is being oxidized and so allows us to calculate the energy more exactly from the oxygen.

There are various ways in which it is possible to measure the energy liberated by a man. An obvious way is to put him into a calorimeter in which the heat produced is determined directly. Many calorimeters have been constructed, from time to time, and in various places. They are large and laborious instruments. Some of them, for example that employed in the School of Agriculture at Cambridge, England, are self-recording: but even so they are expensive and inadaptable, and except for special purposes there is little to recommend them. They show a very great lag in giving a reading and it is impossible by any means to follow rapid changes in the body by their use. The only real advantage they possess is that they measure the heat directly, and not indirectly as other methods do. For this reason, the important fact that the processes of an animal's body obey the Principle of the Conservation of Energy could only be established by employing a calorimeter. A man, or an animal, is put into a calorimeter for a long period, all his excreta are measured, and his oxygen used and his carbon dioxide produced are determined. A calculation of the heat is then possible, which is found to agree with that directly observed by the calorimeter. Apart from such experiments, however, the method is little used, and is inferior to others in respect of convenience and even accuracy.

Another method of determining the energy expenditure of a man is by calculation from his diet. This method is valid provided that we know that the subject oxidizes all, and only, the food he is given to eat. Over a long period, in which his body weight has not changed, this method can be employed, but it is useless for ordinary experiments of short duration.

The only generally practicable method is that involving a measurement of the oxygen used by the subject. A measurement of the carbon dioxide by itself is of little use, although some physiologists are continually trying to prove that it is: partly because the energy per liter of carbon dioxide is much less constant than the energy per liter of oxygen, but chiefly because the body is a vast reservoir of carbon dioxide and many liters of it may be driven out by deep breathing, or by exercise involving the liberation of acid in the muscles, which certainly was not formed by oxidation during the interval considered. The carbon dioxide, in conjunction with the oxygen, is under certain circumstances a useful indicator of what foodstuffs are being oxidized. Usually, however, in muscular exercise, the carbon dioxide is rather an indicator of the degree of ventilation of the lungs, and of the acid being produced by the muscles. Oxygen, however, the body cannot store to any considerable extent: it would be difficult to change the amount of oxygen present in the body and blood at any moment by more than a fraction of a liter. And since the energy per liter of oxygen is approximately constant, the oxygen used is a valuable indicator of the energy liberated.

There have been many methods employed for measuring the oxygen consumption. For example a man may sit, or work, in a closed chamber, and the changes which take place in the air during any interval can be determined by delicate methods of gas analysis. For certain purposes this method is a good one, but for general utility it is poor. It "cramps the style" of the subject too much. It requires a large closed chamber which obviously cannot include a running track, or a swimming pool, or even a path to wheel bricks upon. It necessitates extreme precision in the analysis of the air, since the total changes in the chamber during any ordinary period will of necessity be small. And it cannot be used over short intervals.

Another method, more adaptable, involves the use of a closed air system of which the lungs of the subject form a part. The subject (Fig. 1), sitting for example on a bicycle, has a mouthpiece containing valves in his mouth which

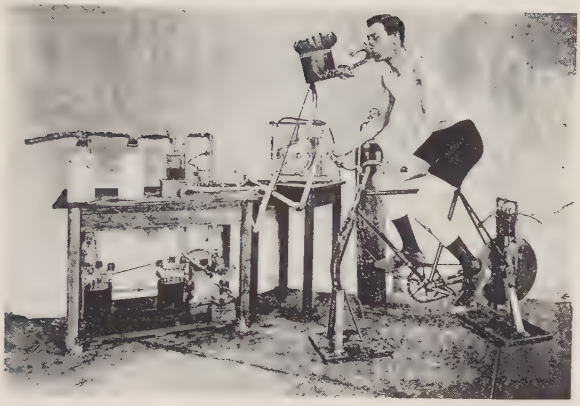

Fig. 1

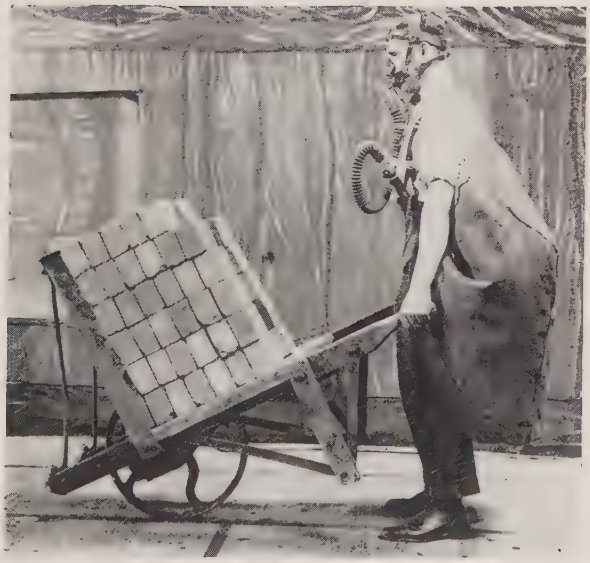

Fig. 2

cause air (1) to come into his lungs from an "inlet" pipe, and (2) to go out from his lungs into an "outlet" pipe. The air circulates around through a closed system in which the carbon dioxide produced is absorbed, and since oxygen is used up, the volume of the system tends to diminish, and oxygen is admitted through a meter to keep the total volume constant. The amount of oxygen used can be determined in this way with considerable accuracy, but again the method in not one of general utility, and cannot be made to yield results over the short intervals that must be employed in the analysis of the changes occurring in really strenuous exertion.

The method which in the study of muscular exercise has made so much possible, is that of collecting the expired air in a bag, or other suitable container, measuring its volume, and analysing its composition. The air of the atmosphere around us is extraordinarily constant: it is

Oxygen	= 20.93%
Carbon dioxide	= 0.03%
Nitrogen and inert gases	= 79.04%

Imagine that a man breathes in 100 liters of air, reckoned dry and under standard conditions, and that his expired air contains,

Oxygen	16.93%
Carbon dioxide	4.03%
Nitrogen	79.04%

as revealed by careful determination with the Haldane gas analysis apparatus. Then it is obvious that he has consumed 4 liters of oxygen in the interval considered and has produced 4 liters of carbon dioxide.

This method is more easily described with the aid of Fig. 2. A subject carries a mouthpiece equipped with inlet and outlet valves, and wears a nose-clip to prevent him breathing through the nose. The weight of the mouthpiece may be carried by a skeleton cap. The atmospheric air in Fig. 2 comes from above, the expired air goes out down the pipe into the bag. Between pipe and bag is a tap with a side-hole, enabling the expired air to escape to the

atmosphere till the tap is turned, when it passes into the bag during any desired interval. The bag may be carried on the back during work, Fig. 2, or it may rest upon the ground by the subjects side during recovery, Fig. 3. Or a series of bags may be employed, Fig. 4, for following the rapidly changing events which occur during the early stages of exercise, or when exercise suddenly ends. In Fig. 4, six small bags and one big bag are shown, each connected with its tap. At first, before exercise begins, the expired air escapes to the left. This exit is then closed and the first bag is opened: at the end of the appropriate interval this is closed and the second bag is opened; and so on. Or again a tank, arranged like a gasometer, may be used instead of a bag to collect the expired air. This has various advantages, one of them being that the volume is measured directly by the rise of the inner tank, or the fall of the counterbalancing weight *W*, Fig. 5. *F* is a fan designed to keep the air thoroughly mixed in the inner tank: *T* is the inlet pipe, rising just above the level of the water. By means of this arrangement it is possible to make a continuous series of observations on the oxygen used by a man, during any process in which he can remain within a short distance of the tank. The only advantage, and it is a very important one, of the bags is that they can be carried about and used where desired, even on a moving subject.

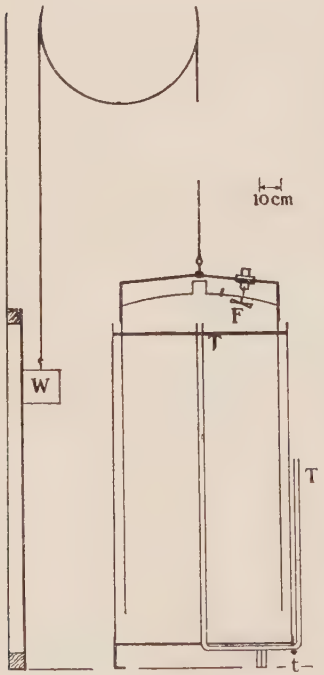

Fig. 5

After collection of the expired air over any interval, its volume is measured, the temperature and pressure are noted, and one or more samples are taken from a side tube into an evacuated sampling bottle for analysis. This proc-

Fig. 3

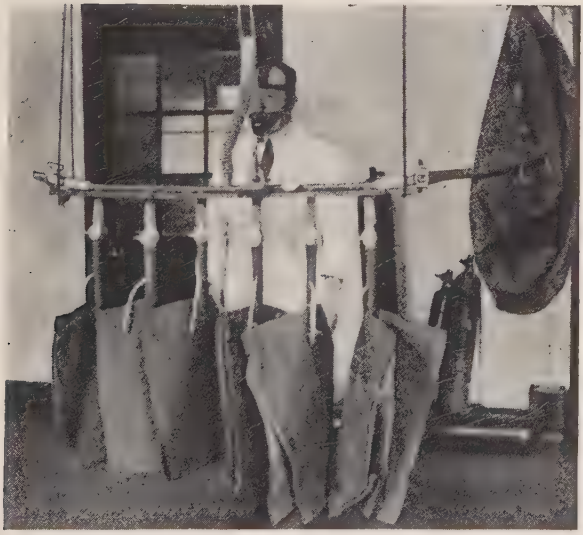

Fig. 4

ess is usually carried out in some form of Haldane gas analysis apparatus. It is not easy, and very great care must be taken or ridiculous results will be obtained. Personally I should feel inclined to mistrust the observations of anyone who does not, at least once a day, analyse pure atmospheric air and get the theoretical value 20.93% for the oxygen. The calculation may then proceed as follows:—

I. The expired air is saturated with water vapor at the temperature and pressure noted. Reduce its volume to dry air at 0°C and 760 mm.

II. We cannot assume that the expired air (which we measure) has the same volume as the inspired air, for the carbon dioxide given out usually has a different volume from the oxygen taken in. We can, however, except under special circumstances, assume that the same amount of "nitrogen" is given out with the expired air as is taken in with the inspired, which will allow us, if we wish, to calculate the volume of inspired air. The following simple formula can be used.

Analysis of Inspired and Expired Air

	Inspired	Expired
Oxygen	20.93%	x%
Carbon dioxide	0.03%	y%
Nitrogen	79.04%	n%
Reduced volume	A liters	B liters

(a) $A \times 79.04 = B \times n$

(b) Oxygen consumed $= B \dfrac{(n \times 0.265 - x)}{100}$ liters

(c) Carbon dioxide produced $= B \dfrac{(y - 0.03)}{100}$ liters

The result, with good analyses and careful measurement of the volumes, should be accurate to about 1 part in 300 or 400. Actually it is sufficient, for most physiological purposes, to read total oxygen consumption to within 1%, so that the method itself is perfectly adequate to its task.

CHAPTER II

Oxygen and Carbon Dioxide: The Steady State of Exercise

WHEN a human subject remains at rest for a long period, 15 to 80 minutes depending upon the severity of the exercise he was previously taking, his rate of oxygen consumption, sometimes called his "metabolism," settles down to a constant value, and his *respiratory quotient* (R.Q.) attains a steady level, characteristic of the foodstuffs which he is oxidizing. For carbohydrate oxidation the R. Q. is unity. For fat it is 0.71. For any mixture of fat and carbohydrate it has some intermediate value. Protein, being composed of amino-acids which are oxidized to urea, carbon dioxide and water, gives about the same R. Q. as fat. The amount of protein being oxidized is usually small as compared with that of carbohydrate and fat, and, if desired, its amount can be determined over any extended period from the nitrogen in the urine.

The resting metabolism gradually falls, during a period of fasting, until about 10 hours after the last meal it reaches a "basal" value characteristic of the individual. The "basal" metabolism may be regarded as the minimum required to maintain the temperature of the subject, and is found to vary as the body surface. For individuals of similar shape it is proportional to $W^{\frac{2}{3}}$, where W is the body weight. It is considerably increased in over-activity of the thyroid gland, where an excess of "thyroxin" is being thrown into the system. Indeed a high basal metabolism may be regarded as a sign of "hyperthyroidism," while conversely, in under-activity of the gland, "hypothyroidism," it is diminished. It is increased by the taking of food. Even glucose has an appreciable effect in raising the rate of oxygen comsumption, and such foods as meat, which require chemical modification in the body after they have been absorbed, produce a considerable rise in the metabolism. For this reason experi-

ments in which a steady resting "baseline" is required should be done sometime after a meal, preferably under "basal" conditions.

For a man of ordinary size, say 150 lbs., the resting ventilation of the lungs is about 6 liters a minute. Of this about 4% is taken into the blood as oxygen, and 3.4% is returned to the air in the lungs as carbon dioxide, the resting R. Q. being, under usual conditions, about 0. 85. Thus the resting oxygen consumption of a man is about 250 cc. per minute, enough to provide about 1.25 Calorie, or enough, if he lost no heat, to raise his body temperature about 1°C in 50 minutes. At rest, such a man would require 1800 Calories per day, about half of what he would need in sedentary work. To carry this oxygen, the blood circulates through the body about once a minute, the "minute-volume" of the heart of a subject at rest being 4 or 5 liters.

In measuring this resting metabolism accurately several precautions must be taken:—

(1) The subject must preferably be accustomed to the procedure. Otherwise he may be excited and his metabolism will rise, or his rate and depth of respiration may be altered. The latter will not much affect the oxygen, but it may largely affect the carbon dioxide.

(2) A sufficient fore-period of complete rest must be allowed: otherwise he may not have recovered completely from previous exertion. The period to be given depends upon the subject, and upon the experience of the observer.

(3) The interval of collection of the expired air should be as long as is convenient, preferably not less than 10 minutes. The resting metabolism is relatively so small—it may be increased 16 times during exercise—that errors due to irregular ventilation of the lungs, etc., may be large if the interval be too short.

The measurement of the carbon dioxide as indicated earlier, is much more precarious than of the oxygen. Carbon dioxide exists in the body, preformed, in large amounts in the form of sodium bicarbonate. One liter of blood contains sodium bicarbonate sufficient to liberate 500 cc. of

carbon dioxide when shaken with acid, and there is every reason to believe that the muscles and other soft tissues of the body, which are in diffusion equilibrium with the blood, contain similar amounts. In the body of a 70 kilogram man there are probably 25 liters of potential carbon dioxide in the form of bicarbonate, enough to account for the basal output of carbon dioxide for nearly 2 hours. During exercise, large quantities of lactic acid ($C_3H_6O_3$: molecular weight 90) are produced: in a man running 100 yards at top speed about 30 grams are produced, 1/3 of a gram-molecule, the equivalent of 7.5 liters of carbon dioxide. Thus the immediate effect of exercise is to drive off large quantities of carbon dioxide which has not been produced at the moment by oxidation. Indeed the carbon dioxide comes off long before the oxidation is completed. Even deep breathing can drive off considerable quantities of carbon dioxide from the blood and tissues. At first sight this is not easy to understand. It requires an enormous amount of shaking with air to turn sodium bicarbonate ($NaHCO_3$) into normal sodium carbonate (Na_2CO_3). The difficulty is solved by the discovery that blood and tissues contain other weak acids ready to combine with the alkali as soon as the carbonic acid leaves it. In blood the chief substance of this kind is haemoglobin which we may write as the undissociated weak acid H Hb. The following equilibria exist in blood

$$H\,Hb \rightleftarrows H^+ + Hb^- \qquad (1)$$

$$CO_2 \leftrightarrows H_2CO_3 \rightleftarrows H^+ + HCO_3^- \qquad (2)$$

$$NaHCO_3 \longrightarrow Na^+ + HCO_3^- \qquad (3)$$

$$NaHb \longrightarrow Na^+ + Hb^- \qquad (4)$$

If we lower the carbon dioxide pressure in the lungs (and consequently in the blood) by deep breathing, reaction (2) goes to the left. This lowers the hydrogen ion concentration so that reaction (1) now goes to the right: the haemoglobin ion is formed which takes the place of the bicarbonate ion, which has disappeared, in equilibrium with fixed amount of alkali present. The net result of deep breathing therefore is that the hydrogen ion concentration falls a little (if pushed to extremes this may lead to a con-

dition of "tetany" in the subject), that large quantities of carbon dioxide come off, and that an equivalent amount of haemoglobin is ionized to take its place in combination with the available alkali.

The same thing happens in the muscles, and in other organs of the body. In these the weak acid is not haemoglobin but the protein of the tissue itself, which can exist either as a sodium (or potassium) salt, or else as the undissociated weak acid. Writing the protein as P we have the equilibrium—

$$Na^+ + HCO_3^- + HP \rightleftarrows Na^+ + P^- + H_2CO_3 \quad (5)$$

If we lower the H_2CO_3 concentration by diminishing the pressure of carbon dioxide through deep breathing, this reaction goes to the right and carbon dioxide comes off, the protein taking its place in combination with the alkali. Since the total amount of weak acid (H_2CO_3 and HP) present is thereby diminished, the tissue becomes more alkaline.

When acid is suddenly liberated in the muscles during exercise it does not really drive the carbon dioxide off directly. It is neutralized by the tissues long before the carbon dioxide has been driven off by enhanced respiration. The neutralization takes place in this way. Some of the protein acid of the tissues is ionized—

$$HP \rightleftarrows H^+ + P^- \quad (6)$$

$$NaP \longrightarrow Na^+ + P^- \quad (7)$$

Imagine a quantity of lactic acid, HL, to be liberated suddenly. This increases the hydrogen ion concentration which drives reaction (6) to the left. This leaves some alkali available to combine with the lactate ion of L^- of the lactic acid, which is thereby neutralized. To write it shortly, the reaction which occurs is:—

$$Na^+ + P^- + H^+ + L^- \longrightarrow HP + Na^+ + L^- \quad (8)$$

Owing, however, to the increase in the amount of undissociated acid, HP, present, the hydrogen ion concentration rises, and this rise is rapidly communicated by diffusion to the blood. The blood passes to the "respiratory

center" in the brain, whose important function is to maintain the hydrogen ion concentration of the blood constant by regulation of the rate and depth of breathing. Breathing is increased, carbon dioxide is swept out by a lowering of the carbon dioxide pressure in the lungs, and the hydrogen ion concentration of blood and tissues returns to normal again. Then, and not till then, does the respiratory center allow the ventilation of the lungs to return to its previous level.

This beautiful mechanism of adjustment, partly physico-chemical, partly nervous, is one of the major discoveries of recent physiology.

Only, therefore, on the assumption that the hydrogen ion concentration of the blood and tissues has remained exactly constant can we use the carbon dioxide output as a measure of the carbon dioxide formation. In general, during the rapid fluctuations and the violent changes of exercise and recovery, the assumption is not justifiable: then we must rather regard the carbon dioxide output as an indicator of acid alterations in the body. Provided, however, that the body is in a really "steady state" of exercise or of rest, or that it returns to the same condition as it was in initially at the end of a complete period of observation, then, and then only, we may take the carbon dioxide output as a measure of the carbon dioxide formation. The respiratory center is an extremely sensitive and effective regulator of hydrogen ion concentration, and may be trusted, at least in trained subjects, to keep the carbon dioxide output steady if the condition of the tissues, in respect of acid formation, is also steady.

During continuous work at a constant speed, the processes of the body gradually work up from the low level characteristic of rest to the high level characteristic of the exercise. The emphasis is on the work "gradually". When the rate of working changes, it is two minutes or more before the rate of intake of oxygen adjusts itself to the new level: the oxygen consumption follows the work and does not cause it. With an automobile engine, the case is different. When the rate of combustion is increased by opening the throttle there is an immediate increase in speed

caused by, and not causing, the increased oxidation. With muscles, work precedes oxidation: with the internal combustion engine oxidation precedes work. Indeed, as we shall see later, the muscle is to be likened rather to a storage battery in its manner of working than to any ordinary machine depending on combustion.

The rate at which the steady state is attained, in respect of oxygen intake, (not in respect of carbon dioxide

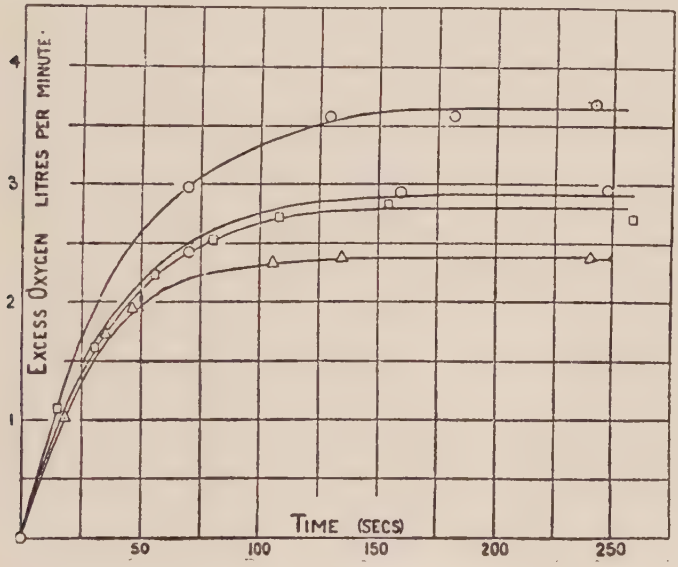

FIG. 6

output, nor probably in respect of lactic acid concentration in blood and muscles) for the case of running is shown in Fig. 6. There are given, horizontally, time from commencing to run; vertically, rate of oxygen intake in excess of the standing rate. The four curves correspond to speeds of 181, 203, 203, and 267 meters per minute (198, 222, 222, 292 yards per minute respectively). For the particular subject studied, the lower three curves represent a genuine steady state. The uppermost curve, however, is not really steady: the exercise was more severe than the subject could tolerate indefinitely, the total oxygen intake (as

shown, plus resting) was at its maximum, and the "oxygen debt" was increasing. Only if we are certain that the oxygen intake is sufficiently low to be well within the capacity of the subject, and that he is not acquiring an "oxygen debt", may we take the measured oxygen intake as truly representing the amount of energy expended during the exercise. When a subject is in a genuine steady state, as he is for example at rest, or during a long walk at constant speed, the oxygen consumption and the carbon dioxide elimination are uniform, the lactic acid concentration in the blood, the heart-rate and its "minute volume," the ventilation of the lungs, even the body temperature of the subject, are all constant, however long, within reasonable limits, the exercise lasts. After these "reasonable limits" are passed, other factors come in. The glycogen reserves of the body are exhausted, there is a low sugar concentration in the blood, stiffness, soreness, blisters may result, and for various reasons the subject may be unable to continue the exercise. The steady state with which we are concerned here is attained within half to three quarters of an hour, often in far less a time, and in these lectures I shall never deal with exertion pushed to the limits where these other secondary factors come in. This is not because such exertion is unimportant. The factors at work in it are seen to advantage in Marathon races and other long-distance events, and they are probably involved in many forms of hard labor in ordinary life. But they are second order terms (to use a mathematical expression) in the physiology of muscle, and in these lectures we will deal with the first approximation only, viz., with those processes which can occur within a few minutes, at any rate within an hour, of the commencement of exercise.

The rate of oxygen intake during a steady state of exercise may rise from 250 cc. per minute at rest to a value of $2\frac{1}{2}$ to $4\frac{1}{2}$ liters, depending on the size, strength and other characteristics of the subject. The highest value ever recorded in one of my experiments was on a Cornell oarsman, rowing on a machine, who after 4.7 minutes had attained an oxygen intake of 4.4 liters per minute, which he maintained for another 6 minutes. He weighed 184 lbs.,

which gave him an advantage. A man of 161 pounds has taken in 4.2 liters per minute while running, which multiplied up in the ratio of 184:161 would be 4.8 liters a minute. Recently a Cornell runner weighing only 147 pounds, has consumed 4.38 liters per minute, which multiplied up in the ratio of 184:147 would be 5.48 liters a minute. This amounts to nearly 30 c.c. per pound or 66 c.c. per kilogram per minute, which is the highest value ever registered. It is unlikely that any man, however big and strong, will get much beyond $5\frac{1}{2}$ liters of oxygen a minute. The factors which decide how much oxygen a man can take in will be considered in a later chapter.

CHAPTER III

Work

THE WORK done by a machine may be measured in ergs, or in kilogram-meters, or in foot-pounds.

1 kilogram-meter = 9.81×10^7 ergs
= 7.23 foot-pounds

Rate of working may be estimated in horse-power, or in kilowatts.

1 kilowatt = 1.34 H. P.
1 H. P. = 33000 foot-pounds per minute,
= 457 kilogram-meters per minute.

Since one liter of oxygen, used in the combustion of glycogen, liberates 15860 foot-pounds of energy, we may calculate that a man consuming 1 liter of oxygen per minute is liberating total energy at the rate of 0.481 horse-power, while a man of 147 pounds consuming 4.38 liters of oxygen per minute is liberating total energy at the rate of 2.1 horse-power, which is at the rate of 0.0143 H. P. per pound of body weight. This is about the limit to which the human machine can go, while breathing air, and of course it is nowhere near what can be attained by internal combustion engines.

The mechanical efficiency of a machine is the ratio

$$\frac{\text{mechanical work done}}{\text{total energy used}}$$

The following approximate figures may be quoted.

Mechanical Efficiency

Steam engines without condensers	$7\frac{1}{2}\%$
Steam engines with condensers	9 to 19%
Gas engines	14 to 28%
Diesel engines	29 to 35%

In the case of the human body, the mechanical efficiency, under good conditions, may attain a value of 25%. The

mechanical conditions must be good. If a muscle attempts to move a load which is too heavy for it, it will do no mechanical work at all, but it will use the same energy as—indeed more energy than—if it were actually accomplishing work. Its speed of movement must be somewhere near an "optimal" value (see Chapter VII) if it is to attain its highest efficiency. Under such conditions, however, (and in ordinary life, our movements and the tools and appliances we use have often been adjusted by experience to give the most efficient conditions), about 25% of the total energy used may be turned into external mechanical work. Thus a man consuming 4.17 liters of oxygen per minute and liberating total energy at the rate of 2 horse-power may be accomplishing mechanical work at the rate of about half a horse-power. Yandell Henderson has estimated that the Yale crew had to exert 5 H. P. between them to drive their boat at the rate they actually attained, just over a half a horse-power per man, which tells us that the oars and speed must have been adjusted to give somewhere near the maximal efficiency.

The mechanical efficiency with which a human subject performs a given process can be determined, if we know the work he does and the oxygen he uses, from the formula:

$$\text{Efficiency} = \frac{\text{work in foot-pounds}}{(\text{oxygen consumption in liters}) \times 15860}$$

It is usual to subtract from the oxygen consumption in this formula the resting oxygen consumption, which represents processes not involved in work at all.

We have already (Chapter I) considered how the oxygen may be measured: it remains therefore to discuss the determination of the mechanical work.

If a man climbs a staircase or a hill the work is easily estimated: it is merely the weight lifted in pounds multiplied by the height in feet. Some energy may be used in horizontal progression, but this is simply wasted as far as our estimate of the work is concerned. Or a man may pedal a fixed bicycle ("bicycle ergometer", Fig. 1) in the labora-

tory, and the work may be calculated from the formula—
Work = circumference × revolutions × force on rim of wheel.
Or a man may employ his effort in producing kinetic energy either in himself, running or bicycling, or in some moveable object, for example, a flywheel. The work he does is then

$$1/2\ MV^2/32.2 \text{ foot-pounds}$$

where M is the mass of the object moved, in pounds, and V is its velocity in feet per second. There are many ways in which the work may be determined, of which these are only obvious examples.

There are two fundamental difficulties about an estimate of the work:—

(1) That in such movements as horizontal walking the external work may be negligibly small. We shall see in Chapter VII that in such cases the mechanical energy is expended in overcoming resistances in the body and muscles themselves;

(2) That in such movements as going downstairs the work done may be negative. Yet going downstairs we know requires energy. The explanation is that, from the point of view of the muscle, the force exerted, and the time during which it is exerted, are what determine the expenditure of energy, so that (apart from the effects of internal friction which in going upstairs hinders and in going dowstairs aids us) the amount of energy expended will be independent of the direction of movement. The same thing would be true of an electromagnet excited by a current: the energy expended by the current would be independent (to a first approximation) of whether the pole piece were drawn away from, or up to, the poles.

These considerations allow us to make some amusing calculations. How fast can a man climb, per hour, on a hillside with a surface good enough to allow him an efficiency of 20%? Let us assume that he does not exert himself unduly, that his oxygen consumption is only half his maximum value, say 2 liters per minute, 120 liters per

hour. Take his body weight as 160 pounds. 120 liters of oxygen is equivalent to 1,902,000 foot-pounds, of which 20%, namely 380,400, can be turned into mechanical work. He can raise himself therefore 380,400/160 = 2380 feet in the hour, pretty good going. Or again, how many liters of oxygen will a man of 160 pounds require to climb the Woolworth Building (792 feet) in New York? Let us assume that he goes very slowly and that his efficiency therefore is 25%. The work done is 160 × 792 = 126700 foot-pounds. The total energy therefore is 507000 foot-pounds: 32 liters of oxygen at 15860 foot-pounds per liter. How much sugar would he burn as the result of the climb? Thirty grams are oxidized by 22.4 liters. He would require therefore 43 grams, about 1 1/2 ounces. Such a man might have a maximum oxygen consumption of 4 liters per minute: if he could maintain an efficiency of 25% at a speed high enough to allow him to attain that value he might do the climb in 8 minutes without acquiring an "oxygen debt." Actually, if he were to go at so high a speed his efficiency would drop, probably to about 17%; he would require 47 liters of oxygen to supply him with the energy, and he would finish with an "oxygen debt" of 15 liters—about all a man can tolerate[1] (see Chapter IV).

When a muscle works, it produces lactic acid: when it recovers this lactic acid disappears again, under the influence of the oxygen used in recovery. During a steady state of exercise lactic acid is being formed at a rate proportional to the magnitude of the effort made, and is being removed, under the influence of (not by) oxidation at the same rate. If the exercise be more severe than the subject can maintain, and in the early stages before the steady state has set in, the lactic acid is accumulating more rapidly than it is being removed: in recovery all of it disappears. Apparently the lactic acid is to be regarded as a "governor" of oxidation in the body: the higher its concentration the more rapid the oxidation which removes it. If a subject takes exercise at a perfectly uniform rate, for example by walking or running, the lactic acid settles down to a con-

[1] Since the above was written the newspapers have reported that the Woolworth Building has actually been climbed in 9 minutes.

stant concentration in his blood and tissues, and his rate of oxygen consumption becomes constant too. It is then found that the rate of oxygen intake varies about as the square of the lactic acid concentration in his blood (which can be estimated chemically on a sample of blood withdrawn from a vein), so that the "governor" is a very effective one. A 5% increase in its concentration leads to a 10% increase in oxidation. This fact was discovered originally in the isolated muscle, by a study of the recovery heat-production, and it suggests that some bi-molecular reaction, involving two molecules of lactic acid, is the governing factor in determining the speed of oxidation. It is known that in recovery the lactic acid reappears as glycogen: maybe the determining reaction is (lactic acid) + (lactic acid) → hexose, the sugar then being polymerised as glycogen. The suggestion is rather vague, but knowledge of the chemical processes involved in oxidation in muscle is very scanty, and the problem requires the aid of chemists for its elucidation.

The factors determining the rate at which oxygen can be taken into the body are several. They are:

(A) *The partial pressure of oxygen in the lungs.* By deep breathing this is slightly increased, but a considerable effect is produced by supplying a subject, during hard work, with a rich oxygen mixture (say 50% oxygen). By raising the partial pressure the diffusion of oxygen through the lung membranes into the blood capillaries is hastened.

(B) *The oxygen capacity of the blood.* In "normal" individuals 100 cc. of blood can hold, when fully saturated, 18.5 cc. of oxygen combined with haemoglobin. In men in training the value tends to be somewhat higher, while in anaemic people it is less. After acclimatization to high altitudes (for example 15000 feet) it may be increased by as much as 40%. On the campus at Cornell, 1000 feet above sea level, the normal man might be expected to have become "acclimatized" to the extent of a 4% increase in his oxygen capacity, making him 19.2 instead of 18.5 The difference is too small to be measured with accuracy, except perhaps

statistically, and it could make only a very slight difference, when at sea-level, in his capacity for taking in oxygen. To train a man at 8000 or 9000 feet, however, might make a very serious improvement in him, when brought down to sea-level, and until his acclimatization had worn off.

(C) *The utilization coefficient of the oxygen in the blood.* The whole of the oxygen is not taken out of the blood when it passes through a muscle. There is probably an "oxygen vacuum" in an active muscle, but the speed of the capillary circulation is so high, and the partial pressure of oxygen in blood only 25% saturated so low, that the last 25% of the oxygen in the blood returns in the veins to the heart. By opening up an enormous "capillary bed" in the active tissue the blood can be slowed down without diminishing the volume of it passing, but even so the "utilization coefficient" of the oxygen in the blood never seems to rise above about 75%: 70% is probably a nearer estimate of its maximum value, taking the whole circulation into account.

(D) *The "minute volume" of the heart.* By this is meant the amount of blood circulating per minute. It is easy to calculate how enormous this must be. Consider our rowing man with an oxygen intake of 4.4 liters per minute. Assume an oxygen capacity of 18.5 cc. per 100 cc. of blood, and a utilization coefficient of 70%. Then 100 cc. of blood gives up 13 cc. of oxygen each time it passes through the muscles. Thus 4.4 liters of oxygen requires 4.4/.13 = 34 liters of blood to carry it. The total amount of blood in such a man's body is only about 5 liters, so that the blood must circulate about 7 times every minute. Remember also that this 34 liters goes through the heart twice, once through the right and once through the left side, a total of 68 liters of blood through the heart per minute. It is extraordinary that a pump weighing only about a pound can have such an enormous output. From the minimum output so calculated, and from the measured blood pressure, it is possible roughly to calculate the work done by the heart during such activity. Allowing a 20% efficiency we can

then reckon out the oxygen which the heart itself must require. The result shows that *during such activity the heart is consuming as much oxygen as the whole body does when at rest.* Probably one of the factors which limit the capacity of the heart is the amount of blood which can circulate through the coronary system of the heart muscle itself and so supply it with oxygen. This may vary in different people.

From such considerations we see that it is no wonder that the maximum oxygen consumption of a human subject is strictly limited: the wonder is rather that it can attain the values it does.

CHAPTER IV

Recovery

I HAVE several times spoken about "recovery" following exercise, and about the "oxygen debt". Even after quite gentle exercise, well within the capacity of the subject, recovery is necessary, though in this case it is of quite limited extent. There is a lag, as was shown in Fig. 6, in the rise of oxygen intake to the full value characteristic of the exercise undertaken, and there is a corresponding lag in the fall of oxygen intake at the end of exercise. (See Fig. 7.) When exercise commences there is a

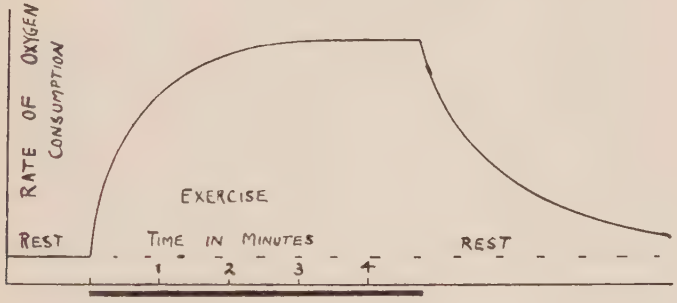

Fig. 7

gradual rise of the lactic acid concentration in blood and muscles to a final steady value, at which a balance exists between formation and removal: when exercise ends there is a gradual return of the lactic acid concentration to the low level characteristics of rest. The removal of lactic acid—its restoration to its precursor glycogen—is a process requiring energy, and this is supplied by oxidation during recovery.

When exercise is more severe than can be met out of energy obtained concurrently by oxidation—owing to the limitation of the oxygen supply, Chapter III—the recovery process may be much more extensive. By "oxygen debt"

is meant the amount of oxygen used, in excess of the resting level, during the period commencing at the moment exercise ends and ending when recovery is complete—for example when the oxygen intake has returned to its resting level. The oxygen used in recovery is employed in the removal of lactic acid, in its resynthesis to its precursor glycogen: and it will be shown later that 1 liter of oxygen used in recovery inplies the removal of about 6 grams of lactic acid. Exercise may be taken far more strenuous than can be accounted for even by the maximum oxygen supply in man. For example, even an ordinary middle-aged University Professor can acquire an oxygen debt of 5.5 liters in 13 seconds by running 100 yards at top speed, which corresponds to an oxygen requirement of 25 liters per minute. His maximum oxygen intake is about 4 liters per minute, so that he can exert himself, for a short time, at least six times as strenuously as he could possibly do were he limited to a supply of energy obtained from contemporary oxidation. A first class sprinter could undoubtedly acquire an oxygen debt of 7 liters by running 100 yards in 10 seconds, which means an oxygen requirement of 42 liters a minute, at least 10 times as much as his maximum oxygen intake. Thus we see that muscles are supplied with a mechanism by which energy may be liberated at a very high rate for a short time, without any concurrent use of oxygen. The oxygen is used, after the exertion is over, in effecting a restoration of the system to its previous condition.

A good analogy to a muscle is the electrical equipment of an automobile. For slow steady "exertion," for example the use of the lamps while running, the current may be provided by the dynamo at the expense of energy liberated simultaneously by combustion in the engine. For starting the engine, however, an enormous current has to be taken out of the battery. The mechanism of this supply of energy is anaerobic; it consists essentially in the transference of SO_4 from the solution into the plates. After the engine has been started, the battery is now slowly charged again at the expense of energy liberated by combustion in the engine. In the case of the muscle the chemical reaction on

which this sudden supply of energy is based is the formation of lactic acid (strictly speaking, sodium lactate or potassium lactate) from glycogen. This is an entirely anaerobic process: the oxygen is used later in supplying energy to drive the endothermic action:—

Lactic acid → glycogen

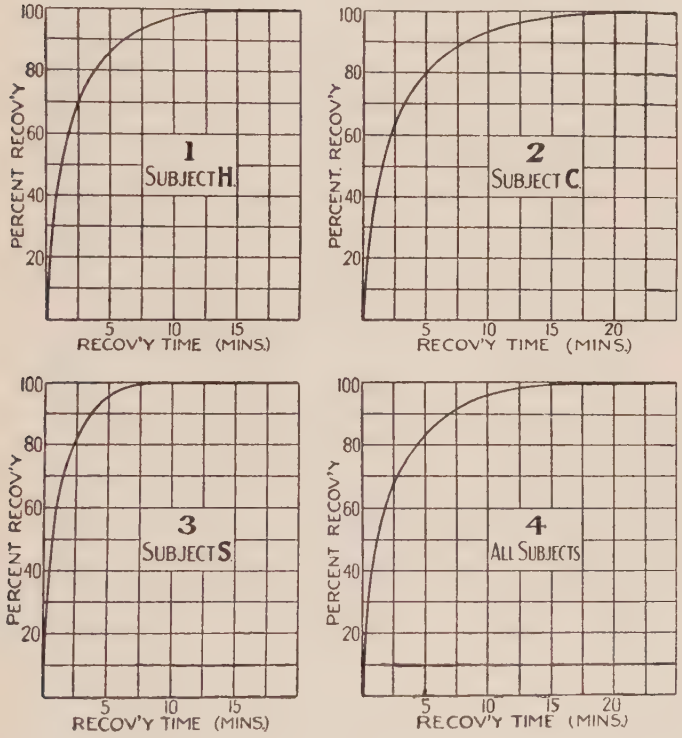

FIG. 8

After gentle exercise of short duration recovery is rapid, and is complete in 2 or 3 minutes. After more violent exercise of short duration it is slower, but still fairly quick. Fig. 8 shows recovery curves of 3 subjects, H., C. and S., and a mean curve for the three, after vigorous "standing running" carried out for 30 seconds or 1 minute. Of the three subjects, H, aged 24, is a fairly good cross-country runner; C, aged 35, is an ex-regular soldier in the

British Army, an "old contemptible" who was gassed during the war and is fairly fit but not very; S is a young American student at University College, London, an extremely powerful swimmer, and a very fit man. S obviously recovers more quickly than the others, H is intermediate, and C slowest, in the order of their obvious fitness. In these curves complete recovery is represented by 100%. At, say, 55% recovery, 55% of the lactic acid liberated by the exertion has been restored as glycogen, 55% of the total oxygen debt has been paid off. Even in C, the slowest of the three, recovery is obviously complete, to all intents and purposes, in 20 minutes. In exercise of the extreme limit of violence, such as sprinting at top speed, even when completed in a short time, for example in 15 seconds, there is evidence that the recovery process is not complete for half an hour or more, at any rate in ordinary men. First class athletes have not yet been studied. The oxygen debt in such cases is quite large, 7 to 8 liters, considerable amounts of lactic acid, 40 to 50 grams, have been liberated, and part of this acid has escaped from the muscles into the blood and has found its way into the tissues of the body at large, from which its removal is a comparatively slow business.

When we come to strenuous exercise maintained for a long time, recovery is still slower. In Fig. 9 is given the case of recovery, expressed as a per cent in the same way as Fig. 8, from the exhausting exercise of running, for 8 to 10 minutes, backwards and forwards at high speed in a short laboratory passage. The curve is a mean from several subjects, all reasonably fit men, University Professors, Instructors, and Students, but by no means first-class athletes. The recovery is obviously much slower, and is not complete until about 70 minutes from the end of the exercise. The body has been flooded with lactic acid owing to the prolongation of the exercise, and its removal takes a considerable time. In very athletic men, especially such people as Marathon runners, recovery would probably be very much more rapid.

The maximum oxygen debt to which the body can submit depends upon various factors: it really is a measure

of the maximum amount of lactic acid which the tissues can tolerate. Such factors are:—

(1) The amount of alkali available, to neutralize the acid, in the protein "buffers" of tissue and blood.

(2) The rate at which the lactic acid is liberated. If this be great, the hydrogen ion concentration in the blood will not rise immediately as high as in the muscles, and consequently respiratory distress will not occur for some

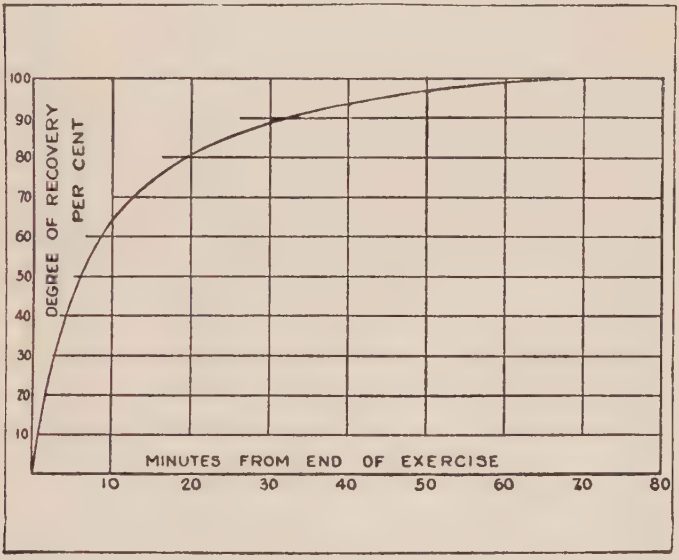

FIG. 9

time after the acid has been liberated because respiratory distress is largely due to acid acting on the nervous system.

(3) The resolution of the subject in pressing his body to exhaustion.

The greatest oxygen debt ever encountered was that on S, referred to above, breathing 50% oxygen at the time. The high pressure of oxygen seemed to relieve the respiratory distress caused by the high hydrogen ion concentration in the blood, and so enabled the subject to press his muscles to a greater degree of exhaustion. The same effect of oxygen is seen in a subject breathing strong oxygen

mixtures high in carbon dioxide. One of my colleagues, in a research, breathed 10% carbon dioxide for an hour by making it up in oxygen instead of air: the respiratory center was greatly excited by the acid effect of the carbon dioxide, but the simultaneous presence of a high pressure of oxygen prevented this from becoming intolerable. Under the influence of oxygen Mr. S (70 kilos = 154 pounds) was able to acquire an oxygen debt of 18.6 liters by "standing running" at top speed in the laboratory, which corresponds to 0.266 liter of oxygen per kilogram of body weight. The amount of lactic acid liberated under such conditions is enormous, about 112 grams. A man of 70 kilos has about 35 kilos of muscle, so that in the above case the subject must have finished with about 0.32% of lactic acid in all the muscles of his body. He was very stiff next day.

This is an extreme case perhaps, but it probably represents the degree of exhaustion obtaining in the members of a boat crew at the end of a 3 or 4 mile race, or in a runner doing his utmost in a race of 440 yards or more, possibly even 300 yards.

In the less able-bodied persons, laboratory workers, etc., who have usually been the subjects of these experiments, the greatest oxygen debt tends to be about .180 liter per kilogram of body weight. Even this means a very fair degree of exhaustion. It represents a total oxygen debt of 12½ liters in a man of 70 kilos (154 lbs.), and a concentration of about 0.21% of lactic acid in his muscles.

Below this upper limit of the oxygen debt any value may be found depending on the vigor and duration of the exertion. In general the highest values are found for extremely violent exercise of quite short duration; indeed I am inclined to believe that the oxygen debt at the end of a 440 yard race would be greater than in any other form of human endeavor.

There is an obvious importance attaching to the considerable size which the oxygen debt can attain. If we wish to know the amount of energy used by the body in undertaking any given task, it is useless merely to measure the oxygen taken in during the work, unless we are quite

certain that the system has attained a genuine steady state. In general it has not, and in carrying out a given task it is necessary to take account of the recovery oxygen as well as of the oxygen consumed during the actual work. Neglect of this fact has made useless a great deal of work done on the subject. The matter is shown diagrammatically in Fig. 10. There we have three cases of exercise: ½ minute of very violent exercise: 2 minutes of moderately severe exercise: and 3 minutes of mild exercise. The oxygen

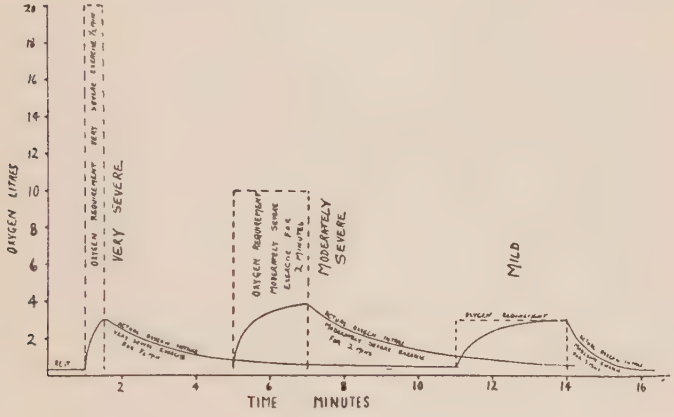

FIG. 10

requirement in each case is represented by the area of the dotted rectangle. The actual intake of oxygen, on the other hand, is given by the full curve, the total area of the oxygen intake curve being equal to that of the oxygen requirement rectangle. Only in the case of the mild exercise is a steady state possible, and this is attained in 2 minutes. In the other cases the oxygen intake remains below the level of the oxygen requirement and the longer the exercise is continued the greater becomes the oxygen debt, the more prolonged the recovery.

Experimentally the measurement of the oxygen requirement is a fairly easy task. The subject precedes the observations by a period of rest sufficient to enable him to recover completely from all previous exertion. Then he equips himself with the apparatus for collecting expired

air, and a resting sample is collected over 10 minutes or more. Then the exercise is taken. If this lasts only for a very short time, as in a 70 yard, or even in a 100 yard run, the subject can hold his breath during the exercise itself, and start collecting his expired air when he finishes. This renders him freer during his effort. For greater durations, however, he must wear the respiration apparatus throughout, and collect his expired air from the moment the exercise begins. The collection is continued for a period suffi-

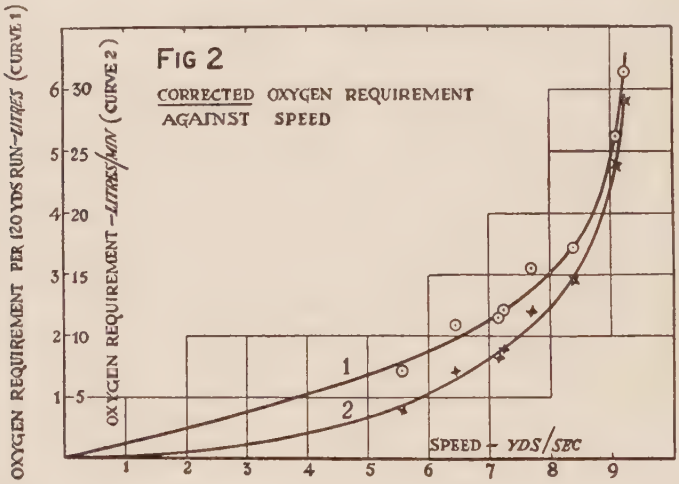

FIG. 11

cient to allow of complete recovery. The oxygen used during exercise and recovery, less that which would have been used during the same period of complete rest, represents the oxygen consumption caused by the exercise, or, as it is called, the "oxygen requirement" of the exercise. This should be a true measure of the energy expended by the body during the process.

An interesting example of oxygen requirement is given in Fig. 11. The quantity measured was the oxygen requirement of running 120 yards at various speeds. The subject was an experienced English athlete, 63 kilos = 139 lbs., capable of running 100 yards in 10 1/5 seconds. He will be referred to further in Chapter VI. Curve 1 gives his oxygen

requirement per 120 yards run. At his highest speed it will be seen that he needs over 6 liters of oxygen, about 100000 foot-pounds of total energy, to complete the distance: at lower speeds very much less. Curve 2 gives his oxygen requirement per minute. At his highest speed this is about 29 liters, 8 to 9 times his maximum oxygen intake. It corresponds to about 14 horse-power of total energy. The curves show how rapidly the energy expenditure varies with the speed. Expressed in mathematical terms, the energy required to run a given distance varies as the 2.8th power of the speed: that required to run for a given time as the 3.8th power

Other examples of the oxygen requirement may be taken. For example, the experiment shown in Fig. 2 was intended to measure the oxygen required, and therefore the energy needed, to wheel a given weight of bricks a given distance. The energy varies with the number of the bricks, and their distribution in the barrow, and also with the speed with which they are moved. For certain conditions the energy per brick moved a given distance is a minimum, and these conditions are those which an employer should arrange for his laborers, in order to secure the minimum of fatigue.

CHAPTER V

Carbon Dioxide

THE SO-CALLED respiratory quotient, CO_2/O_2, indicates the metabolic processes of the body only, as was shown in Chapter III, (1) if the body be in a steady state, or (2) if it return to the same state by the end of a complete period of observation. The fluctuations in the R. Q. are strikingly shown in Figs. 12 and 13. In Fig. 12 the

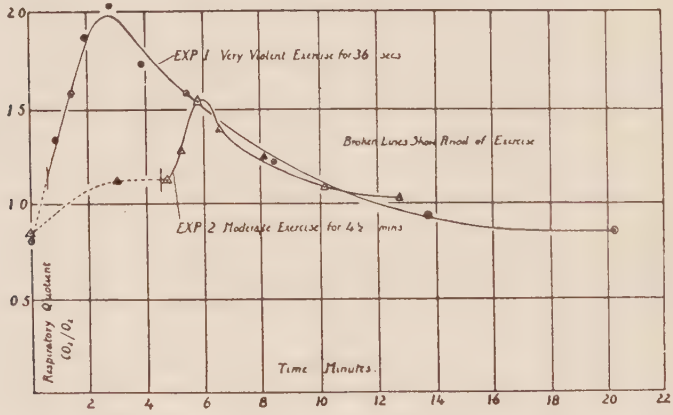

FIG. 12

period of exercise is given by the dotted line, and the R. Q. is seen to rise, during and after the exercise, owing to the excessive lung ventilation produced by the increased hydrogen ion concentration of blood and tissues. A considerable amount of carbon dioxide is driven off in this way, and this has to be taken in again, or rather retained, later on in recovery, in order, as the lactic acid disappears, to enable the tissues to keep their normal hydrogen ion concentration. This retention may last for an extended period, and so long as it continues the R. Q. will be abnormally low. (See Fig. 13.) In one experiment a man, with a previous resting R. Q. of 0.85, showed a R. Q. of 0.59 for a period of

31 minutes, following the violent discharge of carbon dioxide caused by severe exercise. Apart from the simultaneous occurrence of a vigorous transformation of fat into carbohydrate, no true metabolic process could yield such a value, and it is much more likely that the low value found is due simply to a retention of carbon dioxide to maintain the hydrogen ion concentration of the tissues and blood.

The R. Q. of the extra metabolism caused by muscular exercise of not too great severity or duration tends to be about unity, even in an individual kept mainly on a diet of fat.

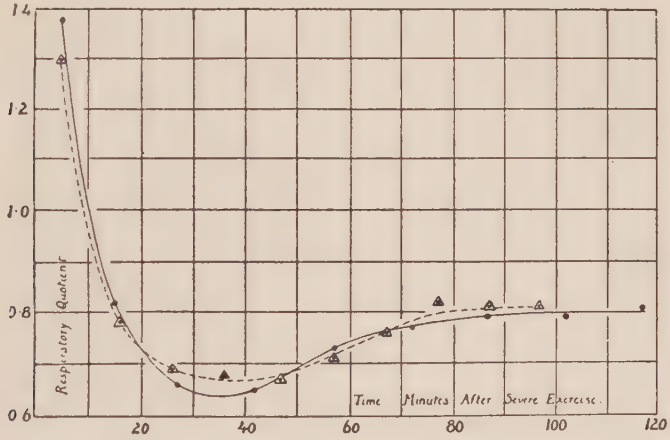

FIG. 13

The experiments must be properly made. A sufficient fore-period must be allowed to bring the body completely to its resting condition. Ten minutes is not sufficient for this: it is advisable to allow 30 or 40 minutes at least. Then a determination of the resting oxygen intake and carbon dioxide output must be made, and since even an experienced subject is apt to alter his rate of breathing on being caused to use a mouthpiece, and to breathe through his mouth instead of his nose, it is well to precede the actual resting determination by a period of at least 10 minutes breathing through the apparatus. Then follows the exercise, with a collection of the expired air, continuing

to the end of complete recovery. The only safe criterion of complete recovery is a fairly exact return to the initial oxygen intake and carbonic acid output. Experience will tell how long a period must be allowed for this: 30 minutes is sufficient after gentle exercise of short duration: severe exercise (such as running 100 yards at top speed) will require 40 or 50 minutes: exhausting exercise may require an hour or more. If a sufficient recovery period be not allowed, irregular results will be obtained. Finally a second determination of the resting oxygen and carbon dioxide is made. If this agrees with the first one, within narrow limits, recovery is complete and the experiment is a good one: if not, the experiment is useless.

The calculation is then made as follows. The whole oxygen used and the whole carbon dioxide produced during the period of work and recovery is determined. Then a mean is taken of the oxygen intake at rest before and after, and a similar mean of the carbon dioxide output. These means are multiplied by the time occupied in work and recovery, and subtracted respectively from the total oxygen and the total carbon dioxide of the work plus recovery period. The differences are the excess oxygen and the excess carbon dioxide due to the work, and the ratio—(excess carbon dioxide): (excess oxygen) is the R. Q. of the excess metabolism due to the exercise.

If the exercise be short, and not too severe, this R. Q. of the excess metabolism is found to be unity. If it be prolonged, the R. Q. falls away from unity towards, but not to, the value obtaining at rest. Even in a subject who has lived on a fat diet for several days, the R. Q. of the excess metabolism of exercise is still unity for short intervals of exercise, though it falls away more rapidly as the exercise is made longer. In diabetic subjects with recent insulin administration (who appear to behave in some ways like a normal subject fed exclusively on fat) the same thing holds. Apparently, even when the stores of it are low, carbohydrate is used preferentially for muscular exercise, or rather for the combustions following exercise. It is probable indeed that muscles really oxidize directly no fuel except sugar, and that other substances are oxidized only

after transformation elsewhere, for example in the liver, into sugar. This, however, is a highly technical and hotly debated matter at present, and justice cannot be done to it here.

When the exercise is of extreme severity, and necessarily therefore of very short duration (for example in a run of 60 to 150 yards at absolutely top speed) a curious thing happens. In this case, even with an extreme application of the precautions outlined above, the R. Q. of the excess metabolism is found to be well above unity, 1.2 to 1.5 for example. There would seem to be no doubt at all of the facts, which were found first during experimental work, described in Chapter IX on the "Efficiency" of sprint running, and then had special experiments devoted to them. It would seem extremely unlikely, though of course not impossible, that the body after exercise of this character should set to work to turn carbohydrate into fat. It would appear far more probable that the basis of the calculation of the "excess R. Q." is at fault. In that calculation we have assumed that the resting metabolism has remained unchanged during the work plus recovery period. If we discard this assumption, it is easier to explain what happens. For a period of 30 to 50 minutes after such severe exercise the *whole* metabolism has a R. Q. of about unity, suggesting that for some reason the body has transferred its oxidation entirely to that of carbohydrate.

Now we know from the work of Cannon and his associates that emotion and excitement cause an increase in the sugar in the blood, which is due partly to nervous impulses reaching the liver, *via* the splanchnic nerves, partly to the liberation of adrenalin in the blood owing to impulses reaching the suprarenal glands. The only likely explanation of the results found would seem to be that the intense physiological excitement of making such an extreme muscular effort has, in this way, caused the mobilization of a considerable amount of sugar (15 to 30 grams) and that in consequence the body oxidizes this, to the exclusion of all other material, until the sugar has been completely burnt.

The emotion and excitement, even the discomfort, preceding a race are well known to athletes. These have probably a sound physiological basis in the activity of the suprarenal glands, whose secretion, adrenalin, places the body in better condition for a violent or exhausting struggle. In experimental work there is little or no excitement preceding the effort, at any rate in an experienced subject, and probably the performance itself will not be so good as under conditions of stress and competition. Nevertheless, as soon as the exercise begins, every function of the body is mobilized for the extreme effort being made, and among these functions are those of the suprarenal glands and their secretion adrenalin, which are seen in this striking rise of the R. Q.

If the exercise be gentle and more prolonged, involving the same total oxygen requirement but spread over a longer interval, this mobilization of sugar does not seem to occur. The excess metabolism only has a R. Q. of unity, the resting metabolism remaining unchanged. It will be interesting to trace out in this way the line which divides effort involving visceral activity from effort involving only the ordinary muscular processes.

CHAPTER VI

Speed and Energy Requirement

THE GREATEST speed at which animals can move their limbs for a very short interval is determined, teleologically, by certain simple dynamical considerations, depending on the strengths of the structures of which the animal is composed. The greatest speed which an animal can maintain for a given time is determined by the considerations of fatigue and energy expenditure which have been outlined in the preceding chapters.

Consider a series of "similar" animals of different size, and let the linear dimensions of any individual be given in the length l. Let M be the mass of one of its limbs, and v the greatest velocity it can attain in that limb. Then its momentum is proportional to Mv. Now this momentum is created at the beginning of a movement, or destroyed at the end of a movement, by a force F, acting for a time t, and we may write

$$Mv = Ft$$

Now t, the time occupied in producing or checking a movement, is proportional to the linear dimensions of the animal, and inversely proportional to the velocity it attains. Neglecting constants we may write

$$t = l/v$$

while M, the mass of the limb, is proportional to the cube of the linear dimensions: so that, again neglecting constants, we have

$$l^3v = F\,l/v$$

Thus

$$v^2 = F/l^2$$

Now the strength of the structures of an animal is proportional to the cross section of its bones, its tendons, and its joints: if the force exerted in starting or stopping be

too great, breakage in these structures will occur. The maximum force, F, therefore, which the animal dare exert is proportional to l^2, say,

$$F = \propto l^2$$

so that

$$v^2 = \propto$$

Thus *the greatest velocity is constant and independent of the linear dimensions of the animal*. In other words, all similar animals, using similar materials for their structures, should have the same maximum linear velocity of movement. This is opposed to one's preconceptions. It would naturally be expected that the larger animal would be the faster. In fact, however, if one looks at animals critically, one finds that the deduction is approximately true. "Similar" animals of course are a mathematical abstraction: the racehorse and the whippet, however, are not so very dissimilar in general design, and they can both go at about the same maximum speed of 40 miles an hour. The dog and the horse can jump about the same height. Even the grasshopper and the kangaroo do not differ in order of quantities in respect of their long jumping capacity. The reason why any animal, including man, is not able to move faster, is that if he did so he would tear his tendons, break his bones, snap his muscles, strain his joints. Indeed one of the problems of an athletic coach is to save his best short-distance runners from doing these very things. Ordinary men have a bigger "factor of safety" than such abnormal specimens, and it is only because they are running much closer to the limits of safety of their structures that some men are much faster than the majority.

The mechanism, the "automatic brake", which prevents too rapid a movement in ordinary men is inherent in the muscle fibres, and is not a property of the nervous system. Its nature will be discussed in Chapter VII and later. General reasoning tells us that such a "governor" or "regulator" of speed must be present in the muscular system of an animal if he is to survive. Special observation is required to describe the actual nature of the mechanism.

It is found that the "governor" in question is a universal and essential part of the muscle machine.

The greatest speed which can be maintained for a given finite time, and not for an instant only, is determined by considerations of energy expenditure. The variation of maximum speed with time during which it can be maintained is well shown in Fig. 14. There are given 4 cases:—

(a) men running,
(b) women running,
(c) men swimming,
(d) women swimming;

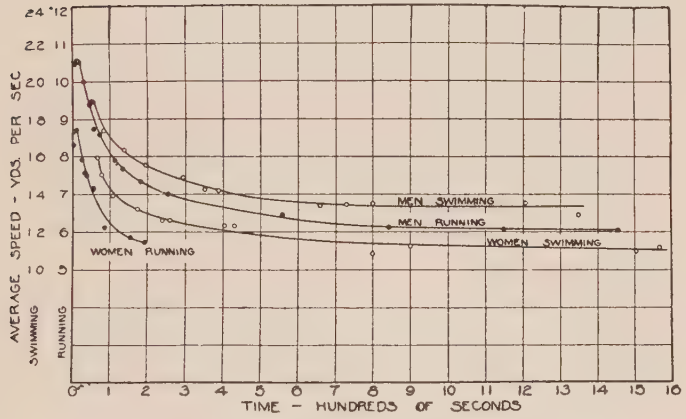

FIG. 14

the plotted points being the world's records, up to 1925, for the various events. Average speed in the race is shown as a function of the time taken in it. Exactly the same type of relation is shown in every case, and it can be deduced, in general, from the considerations outlined above.

To take a simple example:—Imagine a man capable of running up an oxygen debt of 16 liters, and able to take in 4 liters of oxygen a minute through his lungs. The argument is not really as simple as this, but an easy case will make the reasoning more obvious. In one minute he can have 20 liters of oxygen, 4 out of income, 16 on credit. He can run at a very high speed, requiring 20 liters of oxygen a minute (see Fig. 11). In two minutes he can have 24 liters,

8 out of income, 16 on credit: he can spend at the rate of 12 a minute much less than in the previous case, but still fairly fast. In five minutes he can have 36 liters, 20 out of income, 16 on credit: now he can spend at the rate of 7.2 liters per minute, his running must be still slower: and so on. Clearly if he goes a greater distance his oxygen credit of 16 liters has to be spread over a longer interval, and the speed he can maintain will be less.

This method of calculation has been applied to the subject of Fig. 3 by Sargent in a paper in the Proc. Roy. Soc. B. Vol. 100, p. 10, 1926. Making careful and accurate determinations of his maximum oxygen intake, of his maximum oxygen debt, and of his curve (Fig. 11) relating oxygen requirement to speed, it was possible to calculate the speeds at which he could run a series of different races, from 300 yards to 2 miles, the only assumption made being that he would finish completely exhausted. The calculated speeds agreed very closely with those which he knew, by experience, he could attain for the corresponding distances. There was no doubt at all of the general validity of the argument.

Thus, apart from secondary factors, the chief thing which determines the speed at which a given task can be performed, for example, a given distance can be run, is the amount of energy expended. Determine the relation of energy expenditure to speed, the maximum oxygen income and the maximum oxygen debt for the type of exercise undertaken, and assume that the subject is ready to exhaust himself completely, and we have all the data required for our calculation.

CHAPTER VII

The "Viscosity" of Human Muscles

IT REQUIRES, as has been shown in previous chapters, much more energy to run fast than slowly. The reason is simple. If a muscle fiber shortens quickly, it does much less work than if it shortens slowly: consequently if the same external work has to be done, more muscle fibers have to be excited. The mechanism which Nature has provided to prevent us from moving too fast is the same as causes us to do less work if we move more quickly.

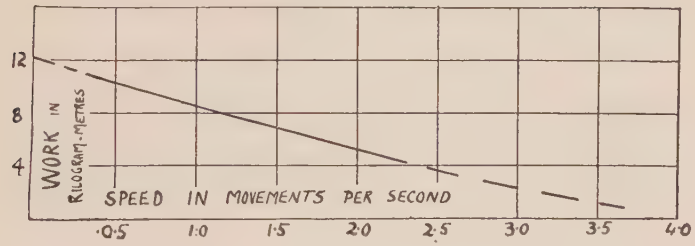

Fig. 15

If the flexor muscles of the human arm be caused voluntarily to contract with their maximal effort, the rate at which flexion occurs will depend upon the load to which they are opposed. If the load be great, the flexion will be slow, and conversely. If the maximal effort be maintained throughout the shortening, the work done will be found to be greater for larger loads, less for small loads. This is quite different from the case of a simple steel spring where the work will be the same for all. If we relate work done to speed of shortening, we shall find that the work is practically a linear function of the speed, decreasing as the speed increases. In Fig. 15 the speed is given horizontally as the "number of movements per second": not that the movement was actually performed more than once, but

this is a convenient way of expressing the quantity 1/t where t is the time occupied in one movement. The work done is given vertically. At zero speed—infinitely slow, "reversible" shortening—the work is greatest, and steadily diminishes with increasing speed, until at about 4 "movements per second" (0.25 sec. per movement) no work at all can be done. At this highest speed the muscles can only just overcome their own intrinsic resistance.

The work done by a human muscle in shortening can be expressed as a simple function of the speed. Imagine a set of muscles, the flexors of the arm, for example, to make their greatest possible effort, so that if they shortened infinitely slowly ("reversibly") they would do work W_o. Now by giving them a lighter load let them shorten with speed v, so that they do work W, which will be found to be less than W_o although they are making their greatest possible effort. Then W is related to v by the equation

$$W = W_o(1 - kv)$$

where k is a constant: 1/k is actually the greatest possible velocity of shortening of the unloaded muscle. This equation can be verified experimentally with human arm muscles and expresses a relation which would hold were there a resistance to rapid motion of a viscous character inherent in the muscle. When a muscle shortens it changes its shape. Its molecules or parts have to flow into a new configuration. The change is hindered by the hysteresis of the molecular system of the muscle, or, if we care to put it so, by the "viscosity" of the muscle substance itself. Whatever one calls it, and however one explains it, the fact itself is obvious and of considerable magnitude, and with reasonable accuracy it obeys the above equation. It is easy to make certain important practical deductions from it. The theory of the effect will be discussed later.

We have considered above the case only of a "greatest possible" effort. The sole reason for so doing is an experimental one, namely, that this is the only constant muscular effort which it is practicable to reproduce exactly. It is not possible in an experimental animal, nor is it possible experimentally in man, to reproduce a muscular effort

equal to any constant fraction of the maximal one. If, however, we could cause only half, or one third, of the fibers of a muscle to contract actively, then the same equation

$$W = W_o(1 - kv)$$

would be found to hold, and in this case W_o and W would have one half, or one third, of their maximal values. Let us imagine that we have to lift a constant load, or to overcome a constant force, at various different speeds. At a low speed a small number of muscle fibers will be sufficient to undertake the task, since, shortening slowly, they all will do a large fraction of their maximal work. At a higher speed a larger number of muscle fibers will be required, since each, shortening more quickly, will do less work. At some high speed all the fibers will be required, since each will do very little work: this is the highest speed at which the given task can be carried out. Let the work to be done be W, and let the "reversible" work of each fiber be w_o. Let n fibers be required to do the work at speed v. Then we have

$$W = nw_o(1 - kv)$$

from which the number of fibers required can be calculated,

$$n = \frac{W}{w_o(1 - kv)}$$

The number n is adjusted by the nervous system to fit the load and the desired speed of movement. We see that as v becomes larger, $(1 - kv)$ tends towards zero, and the number of fibers required becomes very large. Thus a task W which may be easy when carried out slowly may become exhausting when carried out rapidly, for the physiological effort is proportional to the number of muscle fibers employed in it. Muscular contraction is an "all-or-none" affair: if a muscle fiber is stimulated at all it responds to its fullest extent, consistent with the conditions obtaining outside it: its response cannot be varied by varying the stimulus. Thus to exert a greater effort requires a greater number of fibers to be thrown into action, and this will result in greater chemical activity, greater fatigue, greater oxygen requirement, in the muscles involved.

For a given load therefore, a greater speed means a greater physiological effort: this, however, may be compensated for practically by a saving of time, since "time is money" and money is energy. Moreover it may be shown that there is an optimum speed, in the sense that at this speed the greatest possible work is done in a given time. If the speed be too low, the larger amount of work done in one movement of given physiological intensity may not compensate for the smaller number of movements: if the speed be too high, the smaller amount of work in one movement of given physiological intensity may more than balance the advantage of a greater number of movements. At some intermediate speed there is a maximum work.

There is another factor involved in such considerations as these, namely, the energy expended by a muscle as a function of the duration of its contraction. Let H be the total energy given out by the muscle, contracting for time t. Then it can be shown by experiments on isolated muscles that the following relation holds approximately,

$$H = A(1 + bt)$$

Of the constants A and b, b is a characteristic of the muscle fiber itself, A is proportional to the effort made. It is obvious that A must be proportional to the number of fibers involved, and it can be shown that A is approximately equal to $2\,nw_0$ where n is the number of fibers and w_0 is the "reversible" work of each of them. Thus we may write

$$H = 2\,nw_0(1 + bt)$$

H is a measure of the physiological effort involved in the contraction, and we see that this effort is greater the greater be the number of fibers required, and the greater the duration of the contraction. Thus if we quicken up the movement of the muscle by exciting more fibers in it we may so reduce the time occupied that less total energy will be used.

The mechanical efficiency, W/H, may be written,

$$\frac{nw_0(1 - k/t)}{2\,nw_0(1 + bt)}$$

Here the numerator is W, with v altered to $1/t$ which is the same thing, and the denominator is H as described above. This becomes

$$\text{Efficiency} = \frac{(1 - k/t)}{2(1 + bt)}$$

If we know k and b, which can both be found by experiment, we can determine the mechanical efficiency at any desired speed. The expression for the efficiency has a maximum, as is easily seen by plotting it: indeed it is obvious, since the efficiency is zero at $t = k$ and again at $t = \infty$, having a positive finite value between these limits. Thus there is a "most efficient" speed, one at which a given task, of whatever kind, involving the doing of a given amount of external mechanical work, can be accomplished with the least expenditure of total energy. This is an important matter for the workman, or for the employer of labor, and although, in a sense, the existence of such a "most efficient" speed is commonly realized, it is good to have the scientific basis for it made clear.

In such forms of exercise as running or walking on the flat there is no external work done, apart from the small amount involved in overcoming air resistance, and there is no "most efficient" speed: the above argument fails. The whole of the mechanical energy liberated is used in overcoming the frictional resistance of the body itself, particularly the "viscosity" of the muscles. Work has to be done in producing kinetic energy in the alternating movements of the limbs. This kinetic energy is proportional to v^2, so that in running at speed v, mechanical energy has to be expended per yard covered proportional to v^2. Now this must be derived from the work W in the equation

$$W = nw_o(1 - kv)$$

so that writing W as av^2, where a is a constant, the physiological effort, per yard covered, is given by

$$nw_o = \frac{av^2}{1 - kv}$$

Thus the oxygen requirement per yard, which is proportional to the physiological effort nw_o, is proportional to

$$\frac{v^2}{1 - kv}$$

while the oxygen requirement per second is proportional to

$$\frac{v^3}{1 - kv}$$

since the number of yards covered per second is proportional to v. We see therefore that the oxygen requirement per second of running should vary more rapidly than the cube of the speed; and this has actually been found. See, for example, Fig. 11, where, according to Sargent, Curve 2 rises approximately as the 3.8th power of the speed. The above argument is only very general and no exact results could be expected from it. As a man changes his speed he is certain to change his stride and style of running. It shows, however, without going into details, why so much more energy is expended in a more rapid run or walk. In general, for an accurate measurement of the energy expenditure of movement, as a function of the speed, the only practicable method is the determination of the oxygen requirement as described above. In one special case, that of a maximal physiological effort as described in Chapter VIII, the mechanical energy expenditure can be determined directly.

CHAPTER VIII

The Dynamics of "Sprint" Running

LET M be the mass of a runner and let us assume that he can exert a maximum force F in propelling himself horizontally on a track. Since, in general, F will be proportional to the weight of the runner, we may write

$$F = f.M.g.$$

where f is a constant of no dimensions characteristic of the build, strength, skill and fitness of the subject. It will be found usually to vary between 0.5 and 1.0. If there were no resistance inherent in the muscles and limbs of the runner, the acceleration would be constant and he would rapidly reach an enormous velocity. Fatigue of course soon comes on, but not so soon as to prevent the attainment of a very high speed. Actually in a trained man fatigue has no effect up to 60 or 70 yards at top speed, and a maximum velocity is usually attained in 30 to 50 yards. The resistance which rapidly brings his velocity to its constant "limiting" value is that due to the "viscosity" of his muscles which we have described in the previous Chapter.

We have shown above that the force inherent in a muscle which resists its rapid shortening is proportional to the speed of its movement: it will clearly, other things being equal, be proportional to the size of the muscle, and for similar individuals to the mass of the body. Thus the "viscous" resistance may be written conveniently as M v/a, where a is a constant and v is the velocity. This is only true for maximal efforts, since for sub-maximal efforts the mass of muscle involved is arbitrary, and the frictional resistance is mainly confined to the active muscle fibers. The quantity a has the dimensions of time.

We are now in a position to write down the equation of motion of our subject, up to the stage when fatigue begins to come in. Let y be the distance run in time t, the subject

being assumed to be exerting himself to the utmost of his powers throughout. The equation is,

$$M \frac{d^2y}{dt^2} = f\,M\,g - \frac{M}{a}\frac{dy}{dt}$$

or dividing by M,

$$\frac{d^2y}{dt^2} = f\,g - \frac{1}{a}\frac{dy}{dt}$$

This equation can be integrated,

$$y = fga\,[t - a\,(1 - e^{-t/a})]$$

and the velocity at any time can be written,

$$\frac{dy}{dt} = fga\,(1 - e^{-t/a})$$

We see that the velocity attains its limiting value, fga, along an exponential curve, and once this limiting value is practically attained, the distance covered increases uniformly with the time: it becomes $y = fga\,(t-a)$. Thus the total time lag in starting, up to the moment when the maximum velocity has been attained, is easily seen to be *a*, so that if our subject were able instantaneously to start up with his full velocity fga he would run any distance of 50 yards or more in *a* seconds less than he does in actual fact.

We have neglected one factor here: the absolute latent period of the subject's movements. It requires a certain time for the order "go" to be signalled to his brain and to be sent back to his muscles, and for these to develop their maximum force in response. Let this latent period be b: b is very small in a trained athlete but may be fairly large in others. The total lag in starting is really $(a + b)$ seconds, and by t in the above equations we must understand the time measured from the moment when the muscles have developed their response to the signal to "go."

It seemed desirable to test this reasoning and these formulae by actual experiments on athletes. The principle adopted was to time trained runners, exerting their maximum effort, over a series of distances along a horizontal

Fig. 16

track. I am very much obliged to Mr. John Moakley and the Cornell athletes whose co-operation has made these experiments possible.

If a plane coil of wire arranged parallel to a track as in Fig. 16 be connected with a galvanometer, and a runner carrying a magnet approach it, the magnet will induce a current in the coil which can be recorded by the galvanometer. The induction from the magnet increases up to the moment when the magnet lies in the "meridian" of the coil, and then diminishes again as the runner moves on. Thus the current which is induced changes sign as the runner passes through the meridian of the coil. With a very rapidly moving galvanometer the record would be a

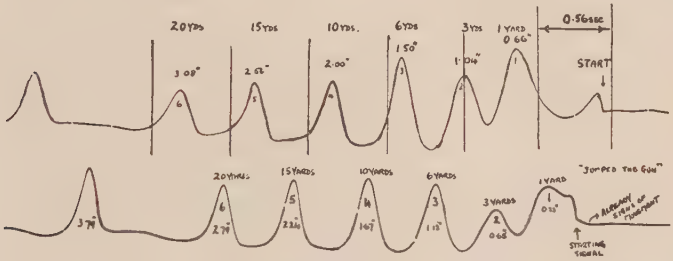

FIG. 17

diphasic one. With an ordinary moving-coil galvanometer, however, which cannot follow such rapid currents, the record appears as a single wave (See Fig. 17) with a sharp point. The more rapid the galvanometer the less lag there will be. In the present experiments the instrument employed has been a Moll moving-coil instrument of complete period 0.8 sec, made by Messrs Kipp en Zonen of Delft, Holland. The top of the wave represents the change over from a positive to a negative induced current, and therefore (with a certain small lag) the moment at which the magnet passes the meridian of the coil. The narrower the coil, and the closer the magnet comes to it, the sharper will be the peak of the wave recorded by the galvanometer.

The coils employed are shown in Fig. 16. They are placed parallel to the track and at intervals along it. In all experiments it is desirable to have a number of them near

the start, so as to determine the initial acceleration of the runner: and in most cases 10 coils have been employed, at distances from the start of 1, 3, 6, 10, 15, 20, 30, 40, 50 and 60 yards. In other cases 15 coils have been used, for studying the onset of fatigue, and these have been placed at 1, 3, 6, 10, 15, 20, 40, 60, 80, 100, 120, 140, 160, 180 and 200 yards. The coils are mounted on stands so that their centers are about chest high. Each of them consists of 200 turns of insulated copper wire, 0.016 inch diameter, and all of them are connected in series with the galvanometer by flexible wire.

The recording arrangements are shown in Fig. 18. A beam of light from a lamp passes through a narrow slit, to give a vertical line of light, and is reflected from the mirror of the galvanometer into a camera. There it is concentrated by a cylindrical lens to a spot, which traces out a line on moving bromide paper. The camera is of the kind commonly employed with the string galvanometer (electro-cardiograph) and is driven by an electric motor. The paper, after exposure, drops through into a box below, where it can be cut off and then taken to the dark room to be developed. A time marker (metronome) cuts off the light momentarily every 1/4 second (about) and so leaves a narrow gap in the record by which the latter can be measured up to the nearest 1/200 second. A pair of typical records is shown in Fig. 17.

The magnet hitherto employed has been merely a hack-saw blade, with its teeth ground off, and magnetized in a solenoid. It is tied round the chest, or the waist, or behind the neck, of the subject with a string or tape. Any suitable magnet, however, would serve. The runner should keep within 1 or $1\frac{1}{2}$ yards of the coils to insure a good sharp record. An athlete carrying a magnet is shown in Fig. 19.

To record the start, an electric switch is opened at the same moment as the signal "go" is given. This breaks the primary circuit in a transformer, and a current is induced in the secondary. To make the record smaller and more sudden, this induced current is put through a second transformer, and the second induced current runs through the

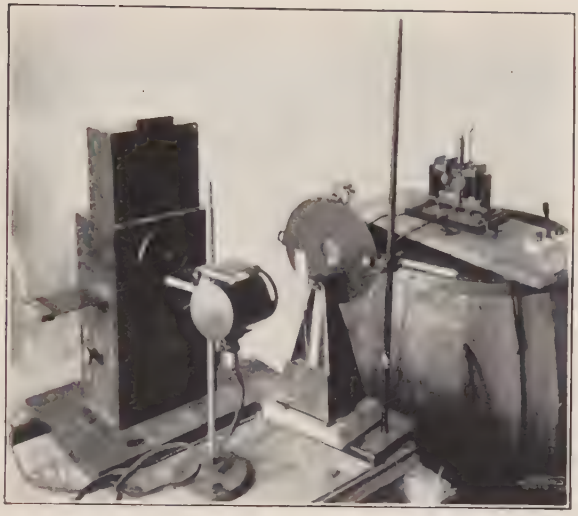

Fig. 18

Fig. 19

galvanometer. The upstroke of the starting signal is extremely sudden and can be read to 0.002 second if desired. If it were required to make the upstroke automatically simultaneous with the order to start, the electric switch could be included in the pistol.

The consistency with which records can be reproduced by a man in training is remarkable. The subject of Fig. 19 ran 4 times in the same afternoon on a board track, at intervals of quarter of an hour, with results given in the following table. (The times given are all about 0.13 second too long owing to lag in the recording system.)

Distance: Yards	1	3	6	10	15
Time: Seconds (1)	0.67	1.09	1.58	2.12	2.72
(2)	0.63	1.07	1.56	2.10	2.72
(3)	0.62	1.04	1.54	2.08	2.71
(4)	0.67	1.07	1.56	2.10	2.70
Mean	0.65	1.07	1.56	2.10	2.72

Distance: Yards	20	30	40	50	60
Time: Seconds (1)	3.30	4.38	5.43	6.51	7.56
(2)	3.28	4.36	5.42	6.51	7.58
(3)	3.27	4.36	5.43	6.53	7.60
(4)	3.27	4.35	5.41	6.48	7.50
Mean	3.28	4.36	5.42	6.51	7.56

The average difference between the mean and the observed time for any distance is only 0.014 second, which is a tribute to the consistency of the human machine.

The chief external force to be overcome in running on the flat is that due to the resistance of the air. At very low speeds this resistance varies as the relative velocity of object and air. At such speeds as we are concerned with in running, and up to 600 or 700 feet per second, it varies as the square of the relative velocity: near, at, and above the velocity of sound it varies still more rapidly. Thus a headwind of 10 miles per hour against a runner going 20 miles per hour will increase the resistance $2\frac{1}{2}$ times. Now it is well known to runners that a head-wind has a slowing effect: a wind of 10 miles per hour may be expected to in-

crease the time in 100 yards by a few tenths of a second. Conversely a following wind is an aid: we may calculate that a wind of 10 miles per hour behind a runner going at 20 miles per hour will reduce the air resistance to ¼, and it is found in practice to diminish the time by a few tenths of a second. The effects, however, which are produced by wind are relatively so small—though of course important enough when it comes to record breaking—that no large part of the resistance which the muscles have to overcome can be attributed to the air. A 2 or 3 per cent decrease in velocity can mean but a very small increase in total resistance. The only other external resistance is that caused by unevennesses in the ground, and this must be negligible on a good track. Thus the main part of the resistance encountered by a man running on the flat must be due to frictional forces inside the mechanism of the body itself. These frictional forces, due either to viscosity or to factors which behave like viscosity, will vary directly as the speed of movement, and so will obey the equation used above to describe the motion of a runner. Any correction to this equation on account of other forces will be so small that, so long as we are dealing with a first approximation only, it can safely be neglected. It is possible, as a matter of fact, to fit the equation to the observations with a high degree of accuracy. Taking fga as 9.43 (in yard-second units) and a as 1.09, and allowing for a lag of 0.12 second, the distances calculated for the observed mean times in the tabulated results given on the preceding page compare with the observed distances as follows:

Observed	1	3	6	10	15	20	30	40	50	60
Calculated	0.97	2.99	6.05	10.07	15.20	20.10	29.9	39.8	50.0	59.9

The average difference between observed and calculated distance is 0.086 yard, that is about 3 inches. No better agreement could be expected. It is obvious that in a short race we may regard an athlete as being propelled by a constant force, and resisted by a force proportional to his speed. Thus, like a raindrop falling through the air, he

rapidly attains a certain limiting speed depending on the ratio of propelling force to resistance, and this speed remains constant until other factors, for example, fatigue, cause it to fall off. The value of fg can be calculated from fga and a by division. On dividing further by g (10.73 yard-second units) we obtain the value of the force exerted in terms of the weight of the man. In the above case the propelling force is 0.806 of the runner's body-weight. The highest value hitherto observed is 0.92, the lowest 0.51. We see, therefore, that the motion of a runner making a maximal effort can be described in terms of two quantities: the propelling force, which is constant, and a resistance proportional to his speed at the moment considered. The propelling force, which we have denoted by fMg, can be determined by an analysis of the distance-time curve recorded in a short run, and from this the mechanical work performed can be calculated. Let l be the horizontal distance run: then the work will be fMgl. Expressing the results in ordinary engineering units, if M be the runner's mass in pounds and l the distance run in feet, the work done will be fMgl foot-poundals, or fMl foot-pounds. If f be 0.85, a value typical of a good short-distance runner, and l be 300 (100 yards), the work done will be 255 M foot-pounds, that is enough to raise his body 255 feet vertically upwards. If M be 160 pounds, this becomes 40800 foot-pounds. If further, the time for the 100 yards be 10 seconds, the work done will be 4080 foot-pounds a second. Now one horse-power is defined as 550 foot-pounds a second: so that such a runner will be developing about 7.4 horse-power of mechanical energy while running at the speed considered. It is obvious why fatigue comes on so rapidly during exercise of this character.

CHAPTER IX

The "Mechanical Efficiency" of the Human Muscle

IT IS interesting to compare the mechanical work done in running with the oxygen used in recovering from the effort. For this purpose the subject is first caused to rest for 45 minutes, and a measurement made of his resting oxygen consumption. Then, without any other exercise, he is required to run 60, 100, or 150 yards at top speed, to pull up as rapidly as possible, and to collect his expired air for 30, 40 or 50 minutes depending on the time needed for complete recovery. Finally a second measurement of his resting oxygen consumption is made, which, for a satisfactory experiment, should be the same as the first. The excess oxygen due to the exercise can then be determined. For the greatest accuracy the subject should not allow any of his expired air to escape, after the moment he starts to run: all of it should be collected. This means that he must hold his breath while running, pulling up, and fixing the mouthpiece in his mouth. This is easy in a 60 yards run, possible in a 100 yards run, very difficult in a 150 yards run. Even, however, if two breaths (say 6 liters) of expired air be lost in the longer distance, this will not be more than 2 per cent of the excess ventilation of the lungs in 30 minutes of recovery, and consequently will produce only a small error. In the shorter distances this error can be completely avoided. Thus, provided that no serious amount of expired air be lost, the exercise can be taken without any impedimenta of mouthpiece and bag, and in the natural way on an ordinary running track. The whole of the oxygen required is taken in during recovery.

A more serious error, and one not so easily avoided, is that due to the pull up. A man running at top speed can stop in about 10 yards, and the effort made in stopping is of a less muscular character than that involved in running, and so should involve less loss of energy. In the experi-

ments made on three different subjects in this connection we have assumed that the effort made in stopping is equivalent to that of running for another 5 yards. It cannot be far from this, for 10 yards of stopping is certainly not as energetic as 10 yards of running at maximum speed. The correction for stopping is reduced in importance by taking a longer distance, such as 150 yards, where it represents a smaller part of the whole.

Another error, also comparatively unimportant, is that due to the onset of fatigue. In 60 or 70 yards the maximum speed, once reached, is maintained to the end. In 150 yards it falls off appreciably, for example 5 per cent in the three able-bodied but untrained subjects of the experiments described.

If we assume that the propelling force fMg diminishes in the same ratio as the speed, we can make an appropriate correction. This again may not be exact, since the "viscosity" also may change with fatigue. But in 60 and 100 yards the correction is negligible, and in 150 yards is comparatively small, so that no great error can result.

We have, therefore, all the data for a comparison of the mechanical output of the muscles with the energy liberated as calculated from the oxygen. With regard to the calculation, it would seem certain that in recovery from exercise such as this the only substance oxidized is carbohydrate, so we may safely take one liter of oxygen as being the equivalent of 15860 foot-pounds of work. Typical results in such an experiment are as follows:

> Subject 161 pounds: distance 60 yards: oxygen used in recovery 3.81 liters: pull up taken as equivalent to 5 yards run: propelling force, calculated from distance-time record, 0.7 of body-weight: work calculated = $161 \times 0.7 \times 65 \times 3 = 22000$ foot-pounds: energy used = $3.81 \times 15860 = 60300$ foot pounds: efficiency = 36.5 per cent.

In the following table, summarized, are all the experiments made in this connection, neglecting none. It is seen that the mechanical work done is, on the average, about 38 per cent of the total energy used. The ratio is not quite

constant, but the complexity of the lengthy observations involved and the many possibilities of error both in the oxygen measurements and in the interpretation of the timing data, are sufficient to warrant a belief that the "mechanical efficiency" of sprint running is really constant at about 38 per cent.

Table

Subject A	Distance	60 yards	Efficiency	36.5	per cent
	"	100 "	"	33.3	" "
	"	100 "	"	29.8	" "
	"	150 "	"	36.7	" "
	"	150 "	"	37.7	" "
	Mean for this subject			35.0	" "

Subject B	Distance 60 yards in all experiments		
	Efficiency	40.1	per cent
		41.6	" "
		36.9	" "
		42.2	" "
		44.5	" "
	Mean	41.1	" "

Subject C	Distance 60 yards in all experiments		
	Efficiency	39.6	per cent
		36.1	" "
		34.9	" "
	Mean	36.9	" "
	Mean of all experiments made		
	Efficiency 37.7 per cent		

The value we have arrived at is of great theoretical interest. In muscle activity, at least in frogs, it is known that of 100 units of energy liberated in the complete cycle, 40 occur anaerobically in the initial process, 60 in recovery. Actually 100 units of energy are set free by oxidation in recovery, of which 60 appear as heat, while 40 go into the latent form of chemical energy in effecting the restoration

of the muscle. Thus if the whole of the initial energy were liberated as mechanical work the efficiency would be 40 per cent. Now in the processes of running a great amount of effort is wasted: the arms are flung about, the legs are pulled violently forward as well as forced back in propelling the body, even the muscles of the face and neck are involved. It seems inconceivable that the muscles involved in pure propulsion should not have an efficiency notably above that of the body as a whole. If they have, that efficiency must be well above 40 per cent: in other words, the mechanical energy they can give out is greater than the whole of the initial energy. There is, as a matter of fact, no theoretical difficulty in this. Many chemical reactions are known in which the free energy, the maximum work, is greater than the total energy. Furthermore, experiments on the isolated muscle readily demonstrate that the area of the tension-length curve (representing the theoretical maximum work) may be greater than the total initial energy as determined by myothermic observation. In the straight fibered muscles of frogs and tortoises the theoretical maximum work in shortening completely from the full resting length is, on the average, 1.22 times the initial heat, giving an overall efficiency of $1.22/2.5 = 48.8$ per cent for the complete cycle of contraction and recovery. It would appear, therefore, that in these comparisons of work and total energy we are coming back, in the case of man, to the same phenomenon as has interested people for a long time in the case of isolated muscle, namely, the very efficient transformation of chemical into mechanical energy in the "initial" process of contraction.

It is well known that in man no actual mechanical efficiency of more than about 25 per cent can be attained: in such processes as bicycling and stair climbing there is an optimum speed at and near which this efficiency is reached. The optimum speed is a compromise between the two factors (a) of "viscosity," which requires a slow movement to get much work, and (b) of energy liberation during maintained contraction, which requires a rapid move-

ment to save time and therefore energy. In discussing the "theoretical maximum work" we have eliminated the time element and imagined a reversible cycle in which viscosity does not affect the result. In dealing with a tension-length curve in the isolated muscle we are obviously doing exactly what an engineer does with his p — v diagram, or a physicist with a Carnot cycle.

We are dealing not with an actual attainable efficiency but with a theoretical maximum. This in fact we are doing also with our runner, for we cannot get a muscle actually to work without showing a "viscous" resistance to motion, and an efficiency of 38 per cent against an external force is possible only if we could. Thus, in this connection, we are dealing with muscular work in man as a thermodynamic problem. This needs emphasis, for it is not, and it cannot be, asserted that the working efficiency of human muscles, against a purely external resistance, is anywhere near the 38 per cent found here. What can be asserted is that this theoretical treatment of the subject is as well justified, and as likely to prove fruitful, as that involving the "reversible process" and the Carnot cycle in physics.

The same high efficiency of transformation of chemical into mechanical energy in the initial process of muscular contraction, can be deduced in a general way from other well-known observations on man. In climbing a staircase an actual efficiency of 25 per cent may be attained at a speed of 1 step in 1.2 second. At speeds far from this the efficiency is lower. Now there are two factors bringing down the efficiency: the work done by a human arm muscle in 1.2 second is only about 75 per cent of the theoretical maximum, owing to "viscosity," and the energy required to maintain a contraction for 1.2 second is considerably more than that needed to keep it up for a short time only. It would seem almost certain that allowance for these two factors would bring the theoretical efficiency of stair climbing to a value at least as high as that deduced for running. The absence of violent extraneous movements, for example of the arms, would tend to make it more

economical than sprint running, and we might expect an appreciably higher efficiency.

It would be possible with a device moving up and down, or backwards and forwards, at any constant speed desired, and carrying an arrangement for writing a tension-length curve on a fixed surface as it moved, to record the greatest work done by a set of human muscles shortening at that speed. If the movement were slow, the work done would be large; if rapid, the work would be small. The theoretical maximum work for zero speed could be obtained by a short extrapolation from the observed relation between work and speed. A device of this kind has been employed by Levin and Wyman for various muscles of lower animals. If the arrangement were designed to repeat itself, back and forth, continuously, a human subject could pull on it during one half of its cycle and so do work, depending on the speed, which would be sufficient to raise his oxygen consumption to a level high enough to measure with accuracy. From the theoretical maximum work, and not the actual work, and from the observed oxygen consumption for fairly rapid shortening, a theoretical efficiency could be calculated from which both factors, viscosity and the expense of maintaining a contraction, would have been eliminated. This has been done for the case of running: here we have eliminated the effect of viscosity, and the movements are rapid and not maintained. The only factor diminishing the efficiency is the presence of extraneous movements, swinging of the arms etc., which do not contribute to the work. By experiments of the kind just indicated, for the case of some simple movement such as flexion of the arm not involving other groups of muscles, it should be possible to do in man by means of oxygen measurement what has already been done in the case of isolated muscles by myothermic observations, namely, determine the absolute maximum of the theoretical efficiency. Such experiments should be made, for they would indicate, more clearly than anything else could do, the ratio of free to total energy in the chemical reactions underlying muscular contraction in the normal working animal.

The above considerations might be applied, with interesting results, to the case of a man running up hill or against a constant measured resistance. The external work would be greater, therefore the speed would have to be less. Let R be the constant resistance: then the equation becomes

$$M\frac{d^2y}{dt^2} = (fMg - R) - \frac{M}{a}\frac{dy}{dt}$$

It is easy to see that the maximum velocity, instead fo being fga, will be

$$a\left(fg - \frac{R}{M}\right)$$

Suppose the subject to run up a slope of 1 in n. n must be fairly large, or otherwise the style of running will be changed: probably a slope of 1 in 10 would be the greatest practicable, possibly even this would be too high. The resistance R is now Mg/n so that the maximum velocity becomes

$$(f - 1/n)\, ga$$

If f were 0.6 and n were 10 this would mean that the velocity would be reduced in the ratio of 6:5. In other words, a subject capable of doing 100 yards in $12\frac{1}{2}$ seconds on the flat would take 15 seconds up such a slope. It would be very interesting to carry out comparative experiments in timing the same subject by the methods described above on tracks of different slopes. To obtain a greater effect, the subject should be one with a small value of f; probably a long-distance runner would prove most suitable. Such experiments would probably provide an interesting confirmation of the theory.

Other experiments of the same kind as those on a runner might be made. For example, a fixed bicycle might carry a very heavy flywheel, or a lighter one very highly geared up. There would be practically no external resistance, since there would be no motion through the air, and the bearings might be made nearly frictionless. Consequently the maximum velocity attained would depend only on the ratio of force exerted to coefficient of viscosity.

There would be the same lag in reaching full speed, owing to inertia, and the equation of motion would be exactly similar. For the analysis, all that would be required would be an accurate record of the number of revolutions of the flywheel as a function of time taken from the start. Such a record would be very easy to make. An analysis would yield the work done, with allowance made for muscle viscosity, and an observation of the oxygen used would be simpler to make than in the case of running, because the subject would be fixed. A flywheel turned by the arms could equally well be used.

In the same way the maximum energy exerted by an oarsman in sculling, or by a crew in an eight-oared boat, could be determined by timing the boat electrically past a series of coils. It would be interesting to see how rapidly a horse could develop its full speed, and thus to calculate the power it is exerting: and to measure its greatest velocity, or that of a whippet. There are obviously many ways in which those interested in sport and animals might contribute to an important scientific problem.

CHAPTER X

Some Applications to Athletics

THE very rapid onset of fatigue during sprint-running, even in the fittest subjects, is well known, and from the above chapters its explanation will be clear: the enormous amount of energy expended in running at top speed tells us that a runner may have gone half way to complete exhaustion within 100 yards. This fatigue is manifested not only by the magnitude of the oxygen debt, but by the slowing up which occurs during a maximal effort continued for more than 7 or 8 seconds. This slowing up is seen in the isolated muscle and is a peripheral effect: it is not to be attributed to "fatigue" in the central nervous system. It is due to a diminished speed of contraction and relaxation, and to an increase in "viscosity" which has been found by Levin and Wyman to occur in the fatigued muscle.

Various experiments have been made at Cornell on a variety of athletes, who have run 200 yards at top speed throughout, being timed every 20 yards along the track. It is necessary to specify that the run is performed at top speed throughout, for the ideal way to run a 200-yards race is to maintain a constant speed, and not to make a maximal effort the whole way. So much energy is wasted by developing an extra 0.5 yard per second in the early stages, that the speed falls, out of proportion, in the later ones. It can be shown mathematically that if the energy expended vary as the 2.8th power of the speed, then it is much more economical, and therefore better, to run, as far as possible, at a constant speed which is rather less than the greatest speed of an unfatigued subject. Athletic coaches realize this, and no 200 or 300 yards runner is advised to make a maximal effort throughout: skill is shown in the choice of speed which will land him at the finish in the minimum time. In practicing for such races the regular use of electrical timing to check the constancy of the speed might

have great advantages. For the present experiments on fatigue, however, to have any meaning, a maximal effort must be made throughout, and a number of subjects have been good enough to volunteer their services. The results are given in Table A. The subjects were as follows:

H.A.R. A first-rate 100 and 220 yards runner
C.M.W. A quarter-miler capable of 50 seconds
O. A half-mile runner
C. A half-mile runner, capable of 2 minutes
S. A mile runner
Ch. A quarter and half-mile runner
B. A first-rate 1 and 2 mile runner
P. A good 2 mile runner
H. Aged 40, once a half-miler similar to C.
F. A poor runner, otherwise healthy and able-bodied.

The average speed of this group of men is given, at different distances, in the last row of Table B. We see that on the average the maximum speed is reached in 70 yards, that then it begins to fall, and by 190 yards has fallen as much as 12%. If we may assume that the rate of energy expenditure of a fatigued muscle at a given speed is the same as that of a fresh muscle at that speed (a definite assumption for which no evidence is at present available), and that (see Chapter VI) the energy liberated per second varies as the 3.8th power of the speed, then a fall of 12% in speed corresponds to a decrease of 39% in rate of liberating energy. Whether the assumption be justifiable or not, the decrease in speed, witnessed in every case, is very obvious.

In the average, widely different individuals have been grouped together. Some information of value comes from taking their cases separately. The most striking performance is that of H.A.R., who having done 100 yards in 9.88 seconds, completed the second 100 yards in 9.57 seconds. He shows a 14% decrease in speed during the last 130 yards. On the other hand B who is a first-rate distance runner, and P. who is a good one, show only a 4½ and a 6% decrease respectively. This is due, no doubt, in part to the fact that these two men are relatively immune to the effects of fatigue, owing to their long-distance running: in

Table A

Time in Seconds for Various Distances in Maximal Effort

Yards	1	3	6	10	15	20	40	60	80	100	120	140	160	180	200
H.A.R.	0.36	0.75	1.205	1.715	2.275	2.760	4.595	6.380	8.125	9.885	11.695	13.550	15.455	17.425	19.455
C.M.W.	0.35	0.76	1.23	1.75	2.34	2.86	4.82	6.75	8.69	10.66	12.70	14.80	16.96	19.17	21.45
O.	0.42	0.83	1.32	1.85	2.46	3.03	5.07	7.10	9.28	11.27	13.39	15.58	17.87	20.19	22.57
C.	0.46	0.88	1.46	1.88	2.50	3.06	5.18	7.25	9.32	11.42	13.52	15.70	17.91	20.22	22.58
S.	0.40	0.86	1.37	1.91	2.56	3.15	5.32	7.45	9.56	11.62	13.87	16.26	18.47	20.90	23.19
Ch.	0.43	0.87	1.35	1.92	2.52	3.09	5.25	7.36	9.50	11.66	13.85	16.08	18.46	20.90	23.46
B.	0.36	0.79	1.29	1.84	2.49	3.09	5.29	7.52	9.72	12.10	14.23	16.51	18.84	21.16	23.56
P.	0.65	1.02	1.55	2.09	2.74	3.33	5.60	7.89	10.11	12.31	14.54	16.81	19.08	21.43	23.79
H.	0.54	1.10	1.64	2.24	2.90	3.54	5.84	8.10	10.39	12.70	15.05	17.47	19.97	22.55	25.27
F.	0.46	0.99		2.27	3.01	3.72	6.48	9.38	12.12	15.02	18.03	21.14	24.30	27.57	30.91

Table B

Speed in Yards per Second at Various Distances

(Note: The speed at 30 yards is taken as the average speed over the interval 20 to 40 yards, etc.)

Yards	30	50	70	90	110	130	150	170	190	Decrease: per cent of maximum
H.A.R.	10.90	11.14	11.46	11.37	11.04	10.78	10.50	10.16	9.85	14
C.M.W.	10.20	10.35	10.30	10.15	9.98	9.52	9.25	9.06	9.77	15
O.	9.8	9.85	9.2	9.6	9.5	9.1	8.7	8.6	8.8	10
C.	9.4	9.7	9.7	9.5	9.5	9.2	9.0	8.7	8.5	12
S.	9.2	9.4	9.5	9.7	8.9	8.5	8.9	8.6	8.4	13
Ch.	9.3	9.5	9.35	9.25	9.15	9.0	8.4	8.2	7.8	18
B.	9.1	9.0	9.1	8.4	9.0	8.8	8.6	8.6	8.7	4½
P.	8.8	8.9	8.9	9.05	8.95	8.8	8.8	8.6	8.5	6
H.	8.7	8.85	8.75	8.65	8.5	8.25	8.0	7.75	7.35	17
F.	7.25	6.8	7.3	6.8	6.6	6.4	6.3	6.1	6.0	18
Average	9.26	9.35	9.36	9.24	9.11	8.83	8.64	8.44	8.26	12

part, also, it is probably due to the economical nature of their running, which fits them for long distance work. Such a test as this might very well be used to indicate promising long distance runners.

It is quite obvious, from such results as these, that the best method of running a 200-yards race is not to go at top speed all the way. Indeed, at anything beyond 100 yards such a method is inadvisable: at 100 yards the falling off of

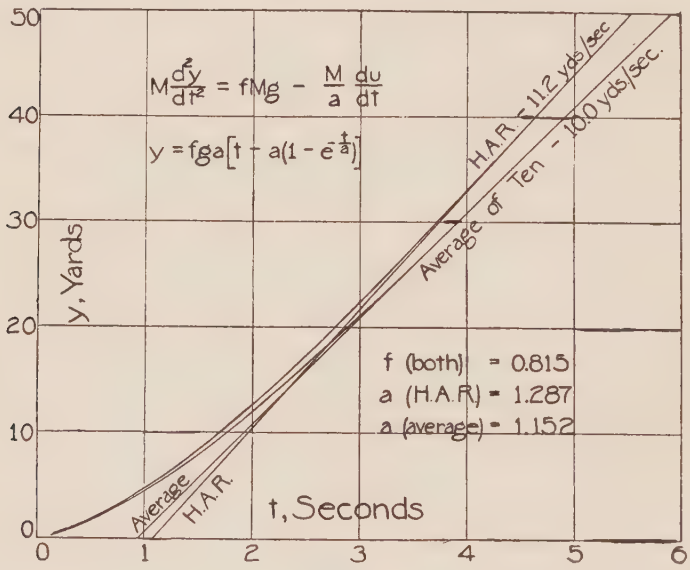

Fig. 20

speed, at any rate in the individuals recorded here, is not sufficient to be of importance.

The subject H.A.R. ran 100 yards on another occasion, when nine other good "sprinters" also were recorded over 60 yards. The average distance-time relation of all 10, including H.A.R., is recorded in Fig. 20, as also is the same relation for H.A.R. alone. The asymptote is drawn to each curve, representing the line of maximum speed. It will be seen that the "average" runner lost 0.94 second in starting up, in the sense that if he had had a flying start at maximum speed, he would, neglecting fatigue, have gained 0.95 second. H.A.R. however lost more, namely, 1.08 second.

This is to be attributed to the fact that he takes longer to attain his maximum speed, and this to the fact that that speed is considerably greater. A mathematical analysis of these two curves, in the sense of Chapter VIII, is of extraordinary interest. The value of f (that is ratio of propelling force to body weight) is practically identical in the two curves: the difference in the curves, and the great superiority (12%) of H.A.R.'s maximum speed, is to be attributed entirely to the constant a. In physical terms, H.A.R. runs faster not because he exerts a greater propelling force, but simply because his internal friction is considerably less. His stride is long and easy, and no doubt part of his success is due to the skill with which he runs. Mainly, however, it is probably to be attributed to the physical characteristics of his muscles, the "viscosity" of which is relatively so low that a high speed is possible. It is interesting to see how the success of a runner may be ultimately due to the physico-chemical properties of his muscle protoplasm.

H.A.R., weighing about 165 pounds, propelling himself 11.46 yards a second, with a force equal to 0.815 of his body weight, is developing about 8.5 horse-power of mechanical energy. In running 100 yards at top speed he does about 40000 foot-pounds of work, which with a 37.7% efficiency (see Chapter IX) must leave him with an oxygen debt of 6.7 liters. This means 40 grams of lactic acid, a production of about 4 grams per second, 1 gram per stride, during running: it is this which causes the fatigue.

In Fig. 21 is shown the timing record made on H.A.R. which is given in Tables A and B on pp. 68 and 69. The distances are shown in yards by the side of, or beneath, the waves. The cross-lines were ruled in afterwards with a T-square, through alternate time-marks made by the metronome shown in Fig. 18. They are 0.683 second apart. The peaks of the waves also are marked in for ease of measurement. The subject was started by a pistol, the starting signal on the record being given by an observer standing near the "starter". This method of recording the start makes the times comparable with those taken by the usual method employing a watch: and assuming that the subject and the

observer recording the start had the same reaction time, it means that the actual start is given by the starting signal.

There is a lag, with the particular galvanometer used, of 0.13 second in the peak of the wave, that is, the peak corresponds to a moment 0.13 second after the subject has passed the meridian of the coil. This is allowed for in the times shown on the record, which are given to the nearest 1/200 second. The record has been cut in three portions, the top being the first, the bottom the last.

It must not be supposed that a superiority, such as that of H.A.R. as a short distance runner, is to be found only in

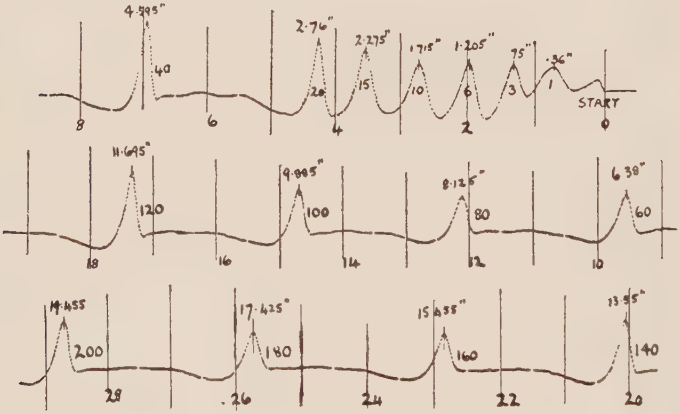

Fig. 21

a lower muscle "viscosity." A higher propelling force might produce a "champion," just as a lower "viscosity" can do, and it would be of great interest to study different types of individuals to see wherein their excellence lies. H.A.R. is typically an easy runner: other men, more muscular then he, might compensate for a greater "viscosity" by a greater propelling force. If they were able to attain the same maximum speed as H.A.R. they would beat him because they would attain it more quickly. On the other hand they would probably tire more quickly also. A series of comparative observations of this kind made, for example, in the heats and finals of the 100 and 200 meters race at the next Olympic games might be of the greatest

interest to physiologists, anthropologists and students of physical training throughout the world. It would be perfectly simple to make such records as that of Fig. 21 on every performer in every "sprint" event. The coils could be placed above the track, and the magnets could be carried on the subject's heads, the induced currents being recorded on a string-galvanometer with many strings, such as was used for sound-ranging during the war. This method would provide permanent records of great value.

Turning to another matter, it is of interest, from the point of view of the circulation rate of the blood, that a runner can consume, per kilogram of body weight, considerably more oxygen than an oarsman. It has always been maintained by physiologists that the efficient circulation of the blood depends largely upon the movements of the muscles, which by alternately pressing on and releasing the veins aid in the return of the blood to the heart. In the case of rowing these movements are never very rapid: in that of running they are very rapid indeed. In oarsmen at Cornell, working at high speed on rowing machines, the following maximal values were recorded after several minutes of maintained effort.

Oarsmen

Subject	Weight lbs.	O_2 liters per min.	O_2 c.c. per lb. per min.	O_2 c.c. per kilo per min.
Bu.	170	4.15	24.4	53.8
H.	184	4.41	24.0	53.0
Bo.	191	4.40	23.0	50.7
S.	185	4.07	22.0	48.5
D.	181	3.92	21.7	47.8
M.	160	3.40	21.3	47.0
T.	170	3.59	21.1	46.5
O's	185	3.60	19.5	42.0
P.	178	3.39	19.3	42.5
Sp.	170	3.23	19.0	41.9

Compare these with the following values obtained on runners, none of whom were as good performers at running as several of the above were as oarsmen.

Runners

Subject	Weight lbs.	O_2 liters per min.	O_2 c.c. per lb. per min.	O_2 c.c. Per. kilo per min.
S.	147	4.38	29.8	65.7
H.	161	4.18	26.0	57.3
F.	106	2.70	25.5	56.2
W.	159	4.00	25.1	55.3
J.	162	4.04	24.9	54.9
L.	153	3.75	24.5	54.0

It is clear that the process of running, owing to its greater ease and the higher frequency of its movements, allows a considerably greater circulation rate of the blood to occur than in the case of rowing, and so presumably is less of a strain to the heart muscle.

CHAPTER XI

Fatigue and Recovery in the Isolated Muscle

IF A PAIR of similar isolated muscles of the same animal, for example the two sartorii of a frog, be placed one in oxygen and the other in nitrogen and stimulated in series by the same succession of electric shocks, about once a second, the one in oxygen will soon attain a steady level of contraction while the one in nitrogen will rapidly reach complete fatigue. In the one in oxygen, a steady state is attained in which the formation of lactic acid from gylcogen is balanced exactly by the restitution of lactic acid to glycogen, under the influence of oxygen diffusing in from outside. In the one in nitrogen, no restitution is possible, and the muscle proceeds to liberate lactic acid until the increasing concentration of that substance finally puts an end to further activity.

That the formation of lactic acid from glycogen during activity is the essential fact about the chemistry of muscular contraction has been shown by a long series of researches, starting from that of Fletcher and Hopkins in 1907, and culminating in those of Meyerhof from 1920 to the present day. In the absence of oxygen the breakdown goes on until the accumulation of lactic acid raises the hydrogen ion concentration to an extent where further stimulation is ineffective. At the same time (Eggleton) an unstable organic phosphate compound breaks down with the liberation of inorganic phosphate: what rôle this phosphate plays is at present uncertain, though the work of Embden, Fiske and others tends to emphasize its importance. It will probably be found that the phosphate is concerned with the mechanism, or the path, by which the glycogen-lactic acid reaction occurs.

This lactic acid does not remain free in the fluid of the muscle: it is rapidly and almost completely neutralized. The resting muscle is a well-buffered system at a pH of

about 7.2, and at such a pH lactic acid is a strong acid, almost completely ionized. Even rigor does not change the pH more than to 6.3, so that complete fatigue produced by stimulation cannot lower it much below 6.7. Therefore practically the whole of the lactic acid set free during stimulation is neutralized: the amount unneutralized is the difference between $10^{-6.7}$N and $10^{-7.2}$N, which is negligible compared with 0.3%, that is 1/30N. The manner of neutralization of the lactic acid was described in ChapterII.

It would seem almost certain that this very obvious production of lactic acid is the chief chemical event associated with contraction. The amount of heat produced when 1 gram of lactic acid is liberated in living muscle is 385 calories. This has been determined many times by direct calorimetrical and chemical methods on isolated frogs' muscles and is fairly accurately known. Of this quantity about 11% may be due to some unknown processes occurring anaerobically, not initially but in the 15 minutes following stimulation. On the probable assumption that this is so, the "initial" heat associated with the formation, in living muscle, of 1 gram of lactic acid, is 89% of 385, or 344 calories. Now the heat of combustion of glycogen dissolved in water is 3836 calories: that of lactic acid is 3601 calories. The heat of formation, therefore, of dissolved lactic acid from dissolved glycogen is 235calories. This leaves 344 − 235 = 109 calories still unaccounted for. The heat of neutralization of 1 gram of lactic acid by a buffered protein mixture is given by Meyerhof as 122 to 138 calories; that by an alkaline salt, $NaHCO_3$ or Na_2HPO_4, as 19 calories. The main part of the neutralization will be carried out at the expense of the protein buffers, part, however, at the expense of the alkaline salts. The amount, 109 calories, still to be explained, clearly falls well within the limits possible if neutralization of the acid be the sole cause of the remaining heat. Hence the initial heat in muscular contraction, which is entirely anaerobic, can be attributed to known chemical reactions, namely, the formation of sodium (or potassium) lactate from glycogen. Thus, if other chemical reactions occur in the initial phase of contraction, they are unimportant from the standpoint

of energetics, as compared with that resulting in the liberation of lactate.

It is not a far step to the hypothesis, which future work may or may not verify, that the liberation of lactic acid is the immediate cause of the contraction. If it be so, we may regard the onset of contraction in the twitch as being due to a new physico-chemical state set up momentarily, before it is neutralized generally, by the local production of lactic acid in relatively high concentration in the neighborhood of surfaces or parts specially sensitive to a change in hydrogen ion concentration. Relaxation we may then picture as neutralization, by the alkali of the tissue at large, of the high local concentration of acid formed by stimulation. This, however, is at present pure hypothesis, and it is safer to admit that we really do not know how the contraction is caused. That the formation of lactic acid is associated quantitatively with the mechanical response of muscle to stimulation would appear certain, and must be reckoned with in any future theory of muscular motion.

Having once been formed and neutralized, the lactic acid merely accumulates, with continued stimulation in the absence of oxygen, until the slowly rising hydrogen ion concentration finally stops the muscle completely and prohibits further activity. In the presence of oxygen, however, the acid disappears, while the glycogen from which it came is restored again to the extent of $\frac{3}{4}$ or $\frac{4}{5}$ of its original amount. In the presence of oxygen there is a delayed production of heat equal to about 1.5 times the initial heat. The following calculation shows exactly how much of the lactic acid is restored and how much is oxidized in the recovery process: or, as it may perhaps better be put, how much glycogen is burnt in restoring the whole of the lactic acid.

Initial heat	1.0
Anaerobic delayed heat	0.12
Aerobic delayed heat	1.5
Total anaerobic heat	1.12
Total aerobic heat	2.5

The above results were obtained by experiments on the heat-production of isolated muscles lying on a thermopile. The total anaerobic heat has an absolute value of 385 calories per gram of lactic acid formed. The total aerobic heat therefore is $\frac{2.5}{1.12} \times 385 = 859$ calories, in a complete cycle in which 1 gram of lactic acid is formed, neutralized, and then abolished in recovery. If the removal of the lactic acid were due simply to oxidation, the total heat in the whole process would be 3836 calories, namely, the heat of oxidation of 1 gram of glycogen. This is about $4\frac{1}{2}$ times as great as the heat actually set free, so that only 0.224 gram of glycogen is actually oxidized in the complete cycle by which one gram of lactic acid is produced and then restored again as glycogen. This result agrees well with actual chemical determinations.

The value so obtained allows us to calculate the amount of lactic acid removed from a muscle in recovery by the use of one liter of oxygen. 22.4 liters oxygen $\equiv$ 30 grams of glycogen oxidized $\equiv \frac{30}{0.224}$ grams of lactic acid removed. Thus 1 liter oxygen $\equiv \frac{30}{22.4 \times 0.224} \equiv 6$ grams of lactic acid removed. Thus we may calculate that an "oxygen debt" of one liter implies the presence in the body of six grams of lactic acid. This value has been used in the calculations given in earlier chapters. Its use assumes that we may apply to human muscles the results obtained in the isolated muscles of the frog. There is much evidence that this assumption is justifiable: probably the same chemical process is involved in all cases.

CHAPTER XII

The Cost of Maintaining a Contraction

IF AN isolated muscle be stimulated by a rapid series of maximal shocks it maintains a contraction, either until fatigue sets in or until the stimulation stops. By making simultaneous measurements of heat and tension developed, for a series of stimulations of various durations, it is possible to construct the experimental relation shown in Fig. 22 for frog's muscle. There are given: horizontally, duration of stimulus: vertically, H_i/Tl, where H_i is initial heat produced in an isometric contraction at length l. l is the "resting" length of the just stretched muscle, and T is the force developed and maintained by it when stimulated. The relation is shown for five different temperatures, and in the little diagram inset the logarithm of the slope of each curve is plotted as a function of the temperature at which it was made.

The effect of temperature is notable; the rate of expenditure of energy in maintaining a contraction of given strength is about doubled by a rise of 10°C. This is obviously to be correlated with the fact that a rise of temperature quickens the individual twitch of which the prolonged contraction is compounded. Any circumstance whatever (for example a difference of species, fatigue, temperature) which causes a prolongation of the single twitch results in the more economical maintenance of a contraction. The slowly moving muscles have this enormous advantage over the rapidly moving ones: a sloth is able to maintain a contraction in his muscles with far less expenditure of energy than, say, a squirrel: and some muscles (the red muscles) of an animal are similarly much more economical than others (the white muscles) of the same animal. The effect of a higher speed in endangering structures (Chapter VI) is not its only disadvantage: it implies also a greater expenditure of energy in maintaining a contraction.

Another notable fact is seen from Fig. 22. All the curves come back to the same point on the vertical axis, namely, $H_i/Tl = 1/5.5$. A long series of researches has been devoted to this matter, (1) because of the importance of the absolute value of this quantity, (2) because of the theoretical significance of its independence of temperature. As regards (1), the result of many determinations shows

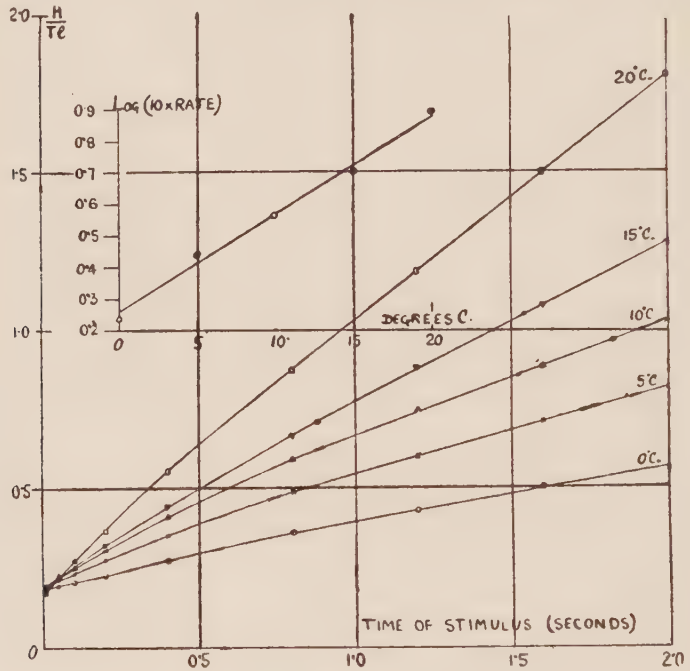

Fig. 22

that the best value to assume for H_i/Tl at $t = 0$ is $1/5$. It will be noted that the force developed, T, is multiplied by the length l of the muscle fibers in order to give a quantity of the same dimensions as the heat H_i. It is obvious that a muscle n-times as long but otherwise the same will develop only the same tension, but n-times as much heat. As regards (2) it is the case that, in a single twitch at a lower temperature, the tension developed is greater, and this has been regarded erroneously as an indication that surface tension, which similarly is greater at a lower temperature,

is the basis of muscular contraction. If the chemical change producing the tension, as measured by H_i the heat, had been constant, or even if Tl/H_i had decreased with a rise of temperature, this might have been regarded as evidence for the surface tension theory: though even then the evidence would have been somewhat flimsy for so far-reaching a conclusion. Obviously, however, if Tl/H_i is independent of temperature, the reason why T is less at a higher temperature may be assumed to be simply that less energy is expended in a twitch at a higher temperature, so that the only evidence in favor of the surface tension theory falls to the ground.

The area of the tension-length curve of a stimulated muscle, representing the theoretical maximum work W_o, is about equal to $Tl/4$ (see Chapter XIII below). Thus for stimuli of very short duration, H_i/Tl being about $1/5$, H_i is equal $0.8\ W_o$. Now it is obvious, from an inspection of the curves of Fig. 22, that the relation between heat and duration of stimulus is practically linear at all temperatures, so that we may write, for the initial heat H_i,

$$H_i = 0.8\ W_o(1 + b\ t)$$

where b is a constant depending on the temperature, nature, and condition of the muscle. If we consider the recovery heat H_r as well, where (Chapter XI)

$$H_r = 1.5\ H_i$$

we may write for the total heat H

$$\begin{aligned} H &= H_r + H_i \\ &= 2.5\ H_i \\ &= 2\ W_o(1 + bt) \end{aligned}$$

It is this formula which we used in Chapter VII. In it, H is the total heat (initial plus recovery) developed isometrically in the just stretched muscle, W_o is the theoretical maximum work as given by the tension-length curve up to that length, t is the duration of the stimulus, and b depends on the nature and condition (temperature etc.) of the muscle fiber. It cannot strictly be assumed, as was done

in Chapter VII, that H is the same when work is done as when the conditions are isometric. The investigations of W. O. Fenn have shown certain complicated relations to exist between work and heat, but since these relations are not properly understood at present, the only thing to do is to adopt the formula above and to recognize that it is only a first approximation to the facts, when one is forced to deal with the case of actual work.

CHAPTER XIII

The Theoretical Maximum Work

IF A MUSCLE be stimulated isometrically at a series of lengths, and its tension recorded, the relation between force developed and length will be as shown in Fig. 23. In a shortening carried out very slowly it is obvious that the muscle can do work equal to $\int T dl$, taken between suitable

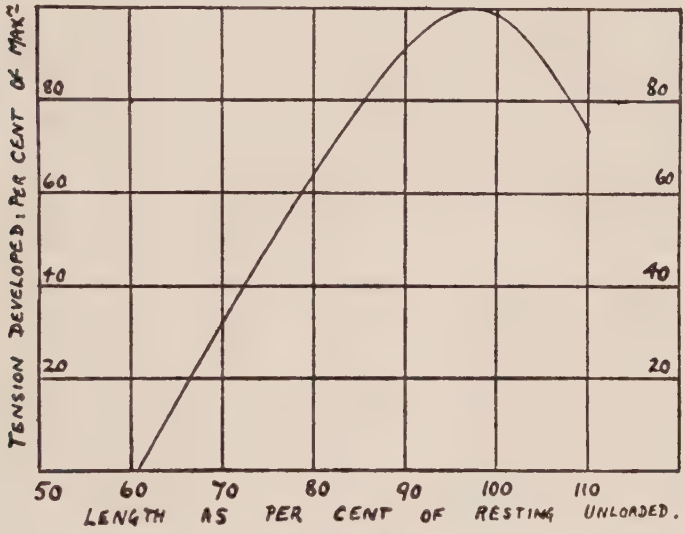

FIG. 23

limits: and the theoretical maximum work of a stimulated muscle at any length l_1, is defined as the value of $\int_{l_2}^{l_1} T dl$ where l_2 is the length at which no further shortening can occur, and no tension is exerted. In order to obtain this actual work it would be necessary to allow the muscle to shorten so slowly that its "viscosity" had no appreciable effect.

The area of the tension length curve, giving the maximum work, is not a simple matter to observe, and it is desirable to connect it with some more easily observable quantities. Let l_o be the length of the muscle when just

stretched out by a minimal weight (it is assumed that the muscle is a straight-fibered one and that the length of the muscle is the same as that of its fibers). Then the force exerted in an isometric contraction is seen in Fig. 23 to be a maximum at, or near, $l = l_o$, and has, let us say, the value $T = T_o$. Then the maximum work W has the following values

l/l_o	$W/T_o l_o$
0.8	.063
0.9	.144
1.0	.244
1.1	.333

Thus, knowing the maximum force T_o which the muscle can develop on stimulation and its full resting length l_o, we can readily find the value of the theoretical maximum work W at any length. The value of W_o, the maximum work at the resting unloaded length l_o, is the one generally referred to in calculations: it must be realized that W_o refers specifically to one particular initial length.

Now it is possible to pass directly from T_o to the initial heat production H_i, and so to find a value for the theoretical efficiency W/H, where $H = 2.5\ H_i$ = initial plus recovery heat. It must be realized, as stated at the end of last Chapter, that H is, strictly speaking, the heat in an isometric contraction, and that if work be actually performed, H, the total energy liberated, will be somewhat altered. Since, however, we have little idea at present what the value of H would be in a contraction with maximal work performed, although it would probably not be very far from that in an isometric contraction, there is nothing to do but to continue our discussion with H as the isometric heat, realizing the weakness in the argument. We know that at $l = l_o$, H_i has the value approximately (see Chapter XII) $T_o l_o/5$;

thus at $l = l_o$ $\quad W/H = \frac{1.22}{2.5} = 0.49$

In a similar way it can be shown that at $l = 1.10\ l_o$, the values of W and H are such that

$$W/H = 0.73$$

The free energy of the oxidation of sugar, on which mus-

cular contraction is based, is almost certainly great enough to allow such values, and even considerably higher ones, for the theoretical mechanical efficiency of the cycle. Thus, in principle, there is no objection to the results obtained for the theoretical mechanical efficiency of the muscle by such a method of treatment.

Many years ago Fick experimenting on this subject realized that by allowing a tetanized muscle to shorten slowly against the inertia of a suitably designed lever, he could get an amount of work not far short of the theoretical maximum: the same thing could be done by employing an ingenious "Winkelhebel" in which the force opposed to the muscle at every length as it shortened was just about equal to the maximum force it could exert at that length. Under ordinary conditions the work was much less than the full amount. The same result approximately is seen in the experiments on human muscles described in Chapter VII: there the contracting muscles were opposed to the inertia of a wheel, and the work they did was absorbed in producing kinetic energy in its mass. The work done was found to obey the relation

$$W = W_o(1 - kv)$$

where v is the velocity of shortening, and W_o the theoretical maximum work for the limits of shortening possible in the intact human arm. For a very large "equivalent mass" in the instrument, that is for a very low velocity of shortening, the work W approximates to the theoretical maximum W_o. W_o could be found in another way, namely, by experiments similar to those described above for the case of the isolated muscle, by making a tension-length curve, and the value of W_o so found would be the same as that determined by the method described in Chapter VII. Thus, with sufficiently slow shortening, that is under conditions of "reversibility" in the thermodynamic sense, the theoretical maximum work can very nearly be obtained as actual work, both for human muscles and for those which have been isolated from an experimental animal. Unless, however, the speed of shortening be very low, the "reversible" conditions no longer obtain, and much less work is done.

CHAPTER XIV

Reversible and Irreversible Phenomena in Muscle

IF A LIVE or a dead muscle be placed upon the junctions of a thermopile with a small weight hanging on it, and a larger weight be gently lowered until it is supported by the muscle, the deflection of the galvanometer registering the temperature of the junctions will follow the course of curve A Fig. 24. If the temperature be allowed to become constant, and the greater weight be gently raised again, the deflection B is now obtained. Both records read from right to left, a rise of temperature being recorded upwards. The initial fall of temperature in B is due to a reversible

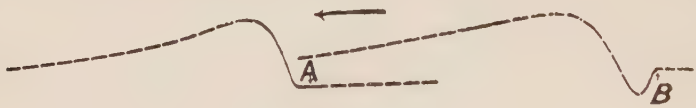

Fig. 24

thermo-elastic effect first described by Weber and studied thermodynamically by Kelvin. The coefficient of thermal expansion of some substances is negative, that is, they shorten on being warmed, and it can be deduced that if they be allowed spontaneously to shorten they will cool. Conversely, if they be stretched they will warm. The initial effect in A also is of this reversible thermodynamic character. Ordinary steel wire, which lengthens on being heated, would show the opposite effects: invar would show no effects at all. The later rise of temperature seen in A and B, both on stretching and releasing, is of an irreversible nature depending upon the viscosity of the resting muscle.

If the weight be lowered and raised alternately, on 1 second, off the next second, for a considerable period as in Fig. 25 (again read from right to left) the reversible effect described above is seen in the little wave superimposed on the main curve, while the irreversible effect (a

production of heat both at "on" and "off") results in the steady displacement from its original zero finally attained by the galvanometer. The irreversible effect is the one with which we are chiefly concerned. On stopping the process of raising and lowering the weight, the irreversible heat production ends and the galvanometer begins

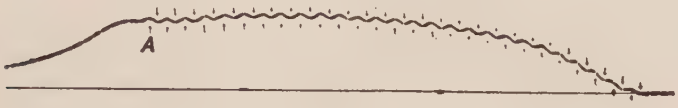

Fig. 25

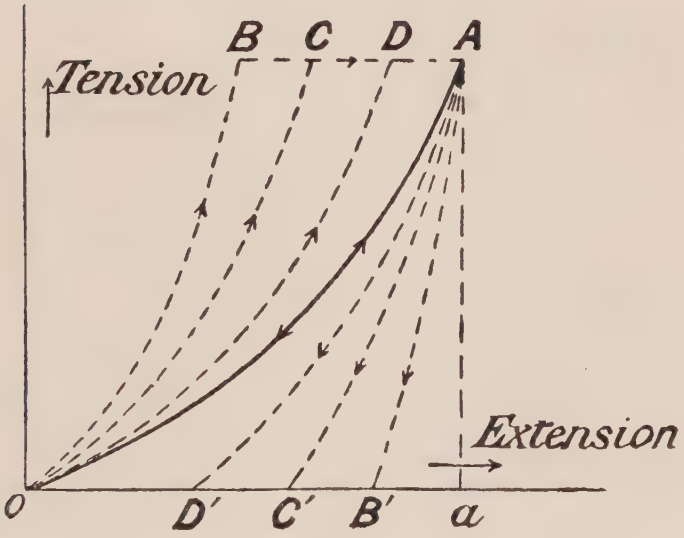

Fig. 26

to return to its base line. This phenomenon is in no way related to the life of the muscle: it occurs in any material showing the phenomenon of "after-extension."

In Fig. 26 OA is the "reversible" tension length curve of a muscle for infinitely slow shortening or extension. *OB* is the tension length relation for a rapid increase of length, *OC* for a less rapid, and *OD* for a still less rapid one. If a weight *P* be lowered on to a muscle at a speed corresponding to *OC*, the work done by the weight in stretch-

ing the muscle will be given by the area between *OC*, *Oa*, and the ordinate from *C*. If the load *P* be left on the muscle, the latter will gradually stretch (it shows "after extension") and further work will be done equal to the area between the ordinates from *C* and *A*. If it be now released at a rate corresponding to the curve *AC'* the work done by the muscle will be equal to the area *AaC'*, the muscle at the end of the release will be longer than when it started, and it will gradually shorten under zero load until its extension becomes *O* again. The total work done on the system during the whole cycle is given by the area *OCAC'O*, which is all degraded into heat: this is the irreversible effect shown in the steady deflection of the galvanometer attained in Fig. 25.

If the inactive muscle be stretched, or released, very slowly, these irreversible phenomena will not occur. The same amount of work will be done by the muscle in shortening as was done on it in stretching, and there will be no balance of work to be degraded into heat. If, however, it be stretched and released at a finite speed more work will be done on it during stretching than by it during shortening, and the balance will appear as heat, as in any hysteresis cycle. Thus the inactive muscle, as indeed almost any colloidal system possessing rigidity, shows phenomena which we may ascribe to the viscosity or hysteresis of its constituent parts in attaining a new geometrical configuration at a finite speed.

In the inactive muscle these "viscous" phenomena, though easily enough discernible, are comparatively small. In the active muscle they play a predominant rôle. If a frog's muscle be attached to a vibrating steel spring, so that the oscillations of the spring alternately stretch and release the muscle, then these will gradually diminish under the damping effect of the viscosity of the muscle. If the muscle be now stimulated, the observed damping will increase many times owing to the increased viscosity of the muscle. In the case of a frog's muscle, the viscosity appears to rise about 20 times as the result of stimulation. In the case of a slowly moving muscle such as that of a tortoise it would increase far more. Here we are getting

into a region where great importance attaches to the effect, and during the last few years it has been very fully investigated. The most conclusive and far reaching experiments are to be published in a paper by my colleagues, Levin and Wyman in Proc. Roy. Soc., B., 1927, but not available at the time of writing. Levin alas! has not lived to see the fruits of his work. He died at Plymouth, while working at the Marine Biological Station, on April 20th 1927. This paper, with Wyman, is a tribute to his unusual experimental skill. Reference to their work will be made in the next chapter.

CHAPTER XV

The Viscosity of Muscle

IT IS NOW possible, by means of methods recently elaborated by Levin and Wyman, to obtain, with precision and ease, the work actually done by a muscle shortening between any specified limits, at any given and constant speed, simply as a tension-length curve. The instrument employed by them is shown in Fig. 27. A beam, rock-

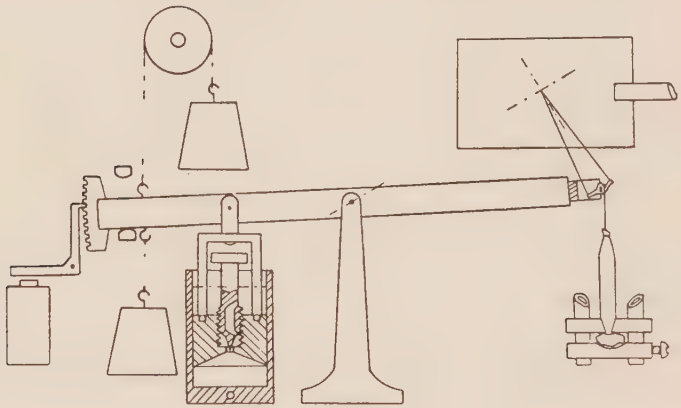

Fig. 27

ing about its middle, is fitted at one end with a very light tension lever to record the force exerted by the muscle shown below. This lever writes upon a fixed surface of smoked glass, making a very fine small record which can be enlarged and copied by placing it in a projection lantern. One co-ordinate, that in the north-west direction in Fig. 27, gives the amount of shortening or lengthening of the muscle, the other, in the north-east direction, the tension exerted by it at the particular moment and length considered. At the other end of the beam is a ratchet arrangement with an electromagnet, by means of which the beam can be held in any desired position and then released

at any required moment. The beam is caused to move up or down, stretching or releasing the muscle by one or other of the weights shown on the left. The speed of stretch or release is governed by the oil dash-pot, supplied with needle-valve, shown below the middle of the left arm of the beam. By adjusting the weights and needle-valve, the speed can be varied from very slow to very fast, and a tension-length curve can thus be written at any desired constant speed of stretch or release.

A muscle is excited by a maximal tetanic stimulus, its tension rises, and when that has attained its maximum the muscle is allowed to shorten between given limits at some

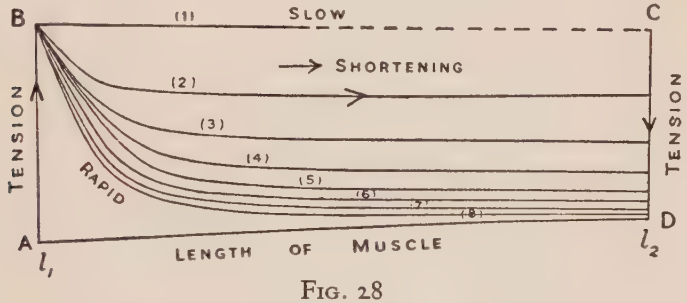

FIG. 28

constant speed; the tetanus is maintained until shortening is complete, when the muscle is allowed to relax. As it shortens it does work, pulling upon the lever which automatically writes a tension-length curve upon the smoked-glass surface. A set of typical records, copied and superimposed, is shown in Fig. 28. The muscle was stimulated isometrically at length l_1, till its maximum tension AB was developed. Then it was allowed to shorten at constant speed to length l_2. There it developed its full isometric tension DC, and the stimulus was stopped. Eight curves are shown for eight different speeds, the bottom curve corresponding to a speed 130 times that of the top one. In arbitrary units these speeds were, respectively, (1) 0.083 (2) 0.59 (3) 1.31 (4) 2.27 (5) 3.79 (6) 5.0 (7) 6.58 (8) 10.85. The very considerable effect of speed is obvious.

The work done, calculated from the area of the curves, may then be plotted against the speed of shortening, and

we obtain a relation shown in Fig. 29. This relation may be determined for any given muscle with great accuracy, and is a characteristic of the particular muscle employed. In respect of the scale of time it varies enormously—hundreds or even thousands of times—from one muscle to another; otherwise, so far as our present knowledge goes, it is invariable in type in all contractile tissues. In quantitative terms, the relative speed of shortening ($\frac{1}{l}\frac{dl}{dt}$ where l is

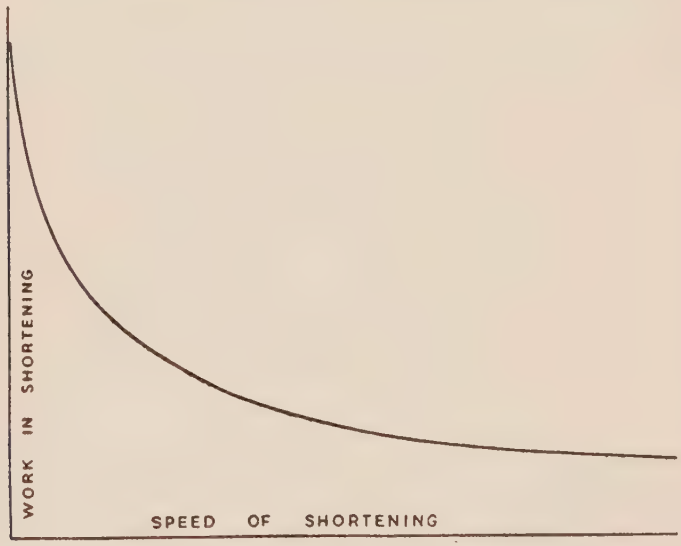

Fig. 29

length and t is time) at which the work is reduced to one-half of its theoretical maximum, varies between the widest limits as we pass from, say, the wing muscles of insects, via frog, man and tortoise, to, say, the smooth muscles of marine invertebrates. In this quantitative factor we have something typical of the individual muscle; in the relation itself, something of a general character. It is clearly of importance to inquire more closely into each.

From the point of view of dealing with these properties mathematically one wished to ascertain the effect of an element of shortening δl carried out instantaneously, for of such elements, occurring at regular intervals δt, any finite

shortening at any finite speed may be regarded as composed. Clearly in the effect on the muscle of a small instantaneous release we might expect to find the simplest expression of the phenomenon in question. Such reasoning led Gasser and me to study the, as it proved, astonishing results of allowing a muscle undergoing an isometric tetanus suddenly to shorten a small distance. Were one to carry out such an experiment with an elastic spring one would find, apart from a few vibrations rapidly damped

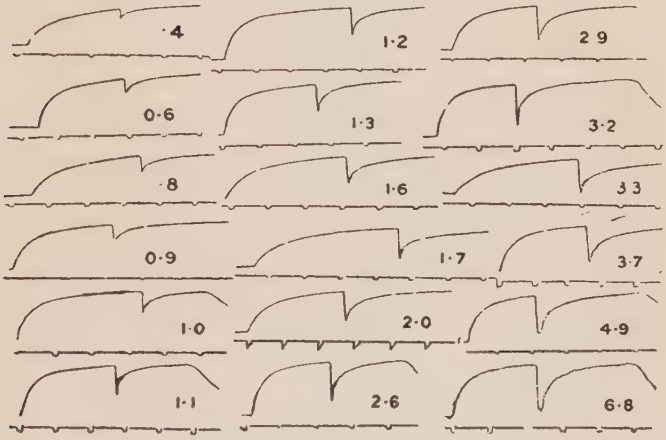

FIG. 30

out, merely a drop from the tension corresponding to the initial to that corresponding to the final length. Not so with the muscle. The tension fell towards zero, and then rose again, but only slowly, to its final equilibrium value. We noticed, moreover, that the curve along which it rose after release was always, within the limits of error of such observations, identical with that along which it rose initially when stimulation began. Recently similar experiments have been carried out upon the slow body muscles of Holothuria. Another series has been performed upon the voluntary muscles of the tortoise, of which some typical results are shown in Fig. 30. There a tetanus was applied isometrically to the long straight biceps cruris muscle of a tortoise (65 mm long, room temperature). The tension

rose and reached a constant level: then a sudden release was allowed corresponding in extent to the number of millimeters shown upon each curve. The tortoise is peculiarly suitable to these experiments owing to the slowness of its movements. It is clear that the process of redeveloping a tension after sudden release is similar in its time relations to the process of developing a tension when stimulation commenced. If so, one cannot but suspect that the processes themselves are the same and not merely their velocities. It is interesting to see where this hypothesis leads.

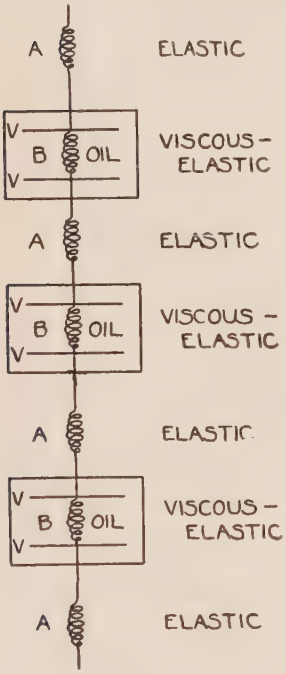

Fig. 31

Imagine a model, Fig. 31, consisting of a series of two different kinds of elements, one simply elastic, the other possessing viscosity as well as elasticity. In the model the elastic element is merely a steel spring A: the viscous-elastic element is a steel spring B attached to vanes V, V, all moving in oil. It must be imagined that the straight wire joining A to B is able to slip freely through a hole in the end of each cylinder. If such a model be slowly stretched, and then suddenly released, the immediate effect will be a shortening of the springs A alone, those in the oil (B) being unable to shorten instantly owing to the viscosity of the oil. Gradually however B will shorten also and take up some of the release from A, so that the tension will gradually rise again as B stretches out A, just as in the muscle shown in Fig. 30. Imagine further that the ultimate contractile elements are those denoted "viscous-elastic," those labelled "elastic" being purely mechanical buffers designed to prevent too sudden a rise of tension when the first kind are excited. Suppose that contraction consists in

a sudden change in the viscous and elastic constants of the viscous-elastic part of the system: for example, in a sudden decrease in the natural length of the spring B, and an increase in viscosity of the oil. Then the external force exerted will not rise instantly, because of the buffer effect of the springs A. The force can only rise as the "viscous elastic" springs B slowly shorten and stretch out the springs A which transmit the force. This is exactly the same thing as we have shown to happen after a sudden release, so that the model would write exactly the same curve when suddenly "excited" as when released and allowed to redevelop its tension. In this respect it shows the same properties as muscle.

Levin and Wyman constructed a model of this kind, and also treated the subject mathematically, and in every respect the behavior of the muscle seems to be paralleled by that of the model. Is one, however, simply to accept the model, and to suppose that on stimulation a new elastic network is constituted, holding between its meshes a viscous fluid, which when the muscle changes its shape has to be forced to flow into a new configuration? At first one did so, perhaps not really believing one's own hypothesis, but confident that for awhile it could be tested and not found wanting, that it could predict results whose verification, or otherwise, would carry one further into the problem. The extreme differences, however, which exist between different muscles, in respect of the speed at which they can shorten and do work, made one become doubtful whether simple viscosity was involved. There are many physico-chemical effects which show an equal dependence upon speed. If one were to assume, in a general way, that the onset of activity in a muscle is accompanied by the formation of some new molecular pattern, either in the surfaces or throughout the volume of the fiber, then one might equally well explain the facts. The equilibrium condition is not always instantaneously reached in a film of molecules packed upon a surface, nor probably is the spatial lattice of a crystalline liquid formed in a moment. The speed of gelation of a protein, involving the arrangement of its molecules in some kind of regular order, may be

slow and largely altered by minute changes in its chemical constitution. In some such way, rather than by invoking simple physical viscosity, one must probably proceed. Viscosity in a sense it is: not gross, but molecular. Molecules do not come instantly into balance with one another, either physically in a surface or a spatial lattice, or chemically in a reversible equilibrium. This slowness of attainment of a final state, involving molecular "viscosity," is a common property of many physico-chemical systems. If such a system be employed for doing mechanical work, this hysteresis will manifest itself as ordinary "viscosity."

Let us return to the consequences of the "quick-release" experiment. At rest, the molecules of the contractile elements of the muscle fiber are in some kind of equilibrium (A) with one another. That this equilibrium may involve, at any rate in striated muscle, some spatial organization analogous to that of a crystalline liquid, is suggested by the presence of doubly-refracting bands visible under the microscope, and recent x-ray observations have tended to show that there is actually a crystalline structure in muscle. As soon as stimulation commences the equilibrium changes from (A) to (B), one factor in the equilibrium being the length of the muscle, another the force which it exerts. The attainment, however, of (B) from (A) is not instantaneous: it proceeds gradually, at a rate depending upon the properties of the molecules involved. Imagine it completed and the muscle then suddenly released. The balance is upset. The molecules are now no longer in proper relation to one another for the shorter length: their spatial patterns must be rebuilt in a different external form. The equilibrium in fact must pass from a state (B) to an analogous but different state (B′). Until that has been done the force exerted cannot attain the steady value characteristic of the final length.

We are dealing with a very general property of equilibria. The time-curve along which a true equilibrium is attained, in a system either without inertia or sufficiently damped by friction, is always analogous to the rise of an isometric contraction in a stimulated muscle, while, if by

any means the position of equilibrium is altered suddenly, the attainment of the new equilibrium proceeds along a similar curve. The phenomena, therefore, which we have found in muscle are old and very familiar: only, viewed aright, they bring the muscle into a very definite physical category.

To take a more specific analogy, consider the packing of molecules in films on the surface of water. Many substances, according to N.K. Adam, show no detectable hysteresis in their compression curves. The molecules have reached their equilibrium pattern in the surface, at a given average area per molecule, before an observation of the surface pressure can be made. Other substances, however, do very definitely show such hysteresis. A striking case is that of films of hyrdolecithin. If the area be suddenly decreased the pressure may at first be several dynes per centimeter greater than the final pressure, to which it falls in several minutes. The fall is approximately exponential in the later stage, being more rapid at first. In the same way, if the area be suddenly increased, the pressure takes a long time to rise to its final value. Equilibrium, however, can finally be attained from either side. Another example is shown in Fig. 32. There are given the compression curves of eicosyl urea, in a monomolecular film on the surface of water, in the neighborhood of the transition temperature. The part of the curve marked with the arrows is at 30.5°C, and it shows a striking hysteresis. The area of the hysteresis loop—the work wasted in going round the cycle—depends upon

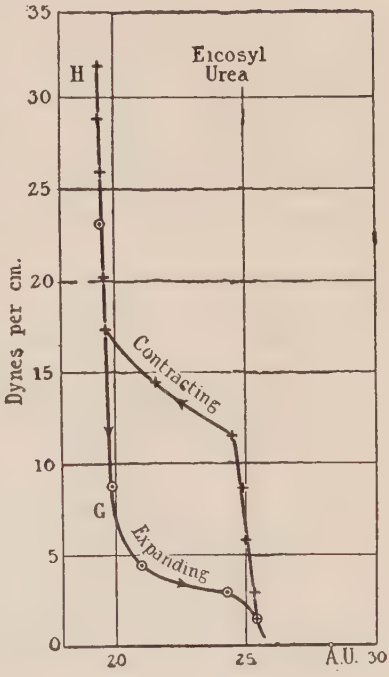

FIG. 32.

the rate at which the compression is applied or removed. The changes with hydrolecithin are exactly similar to those which occur with muscle following either a quick release or a quick stretch, and there can be no doubt that the same thing would happen with any substance showing hysteresis in its compression curve.

In admitting the closeness of the analogy, one does not assert that the contractile process is necessarily concerned only, or at all, with surface forces. What is true of two-dimensional patterns, or rearrangements, must be true also of those requiring three dimensions for their manifestation. The formation of jellies or crystals is often slow: the rate of production of a blood clot may vary widely with minute changes in the constitution of the plasma. The formation of such a structure during stimulation, its disintegration during relaxation, its gradual tightening up, as a preliminary to the development of an external force—in such a picture we may find a very fruitful hypothesis of the contractile process.

These things then are what determine the rate at which a muscle can contract, the speed at which a fly can beat its wings, at which an athlete can run, or a frog can hop. We have been led from the frog to man, and from man to the frog, from both to holothuria and other strange animals of the sea, from holothuria back to the tortoise, and from the tortoise finally to Achilles. And now we see that Achilles himself depends, for the speed at which he can run, upon the rate at which molecules can set themselves in new configurations and patterns in his muscles; which, to many of us, makes him not less interesting, but much more.

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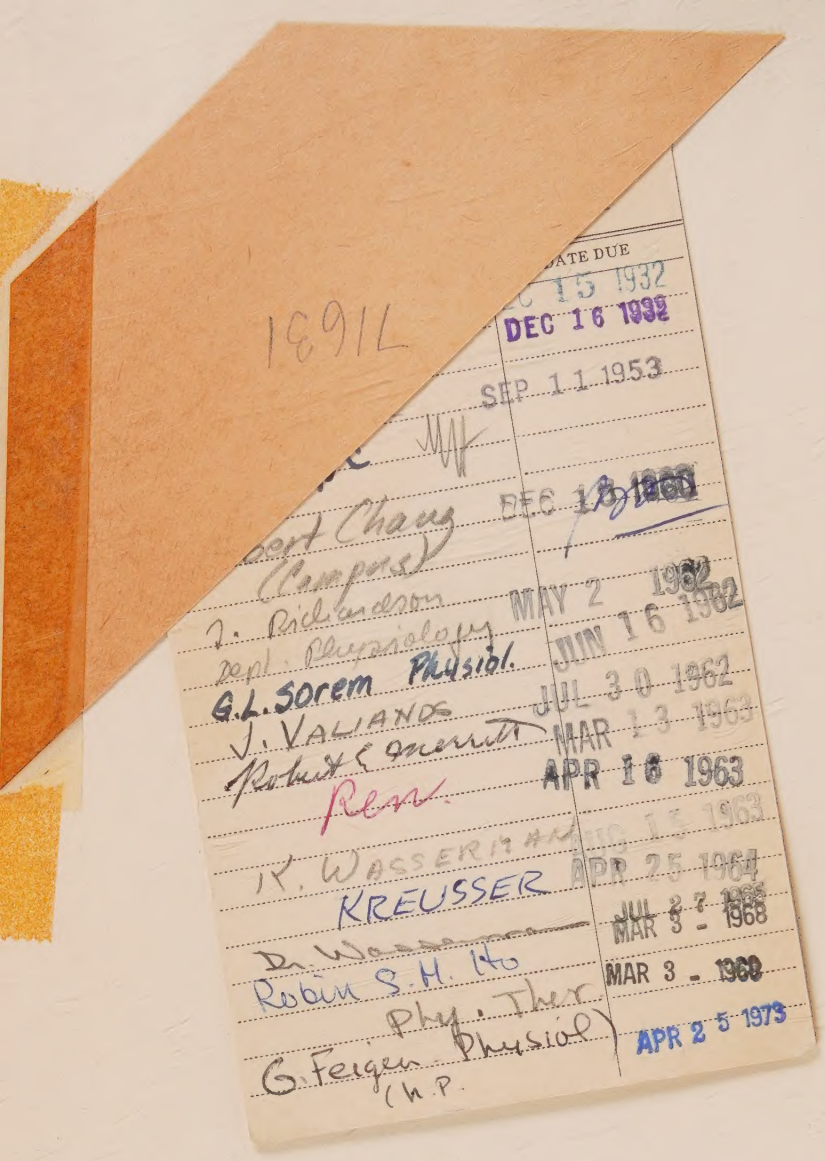
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